The eco-evolutionary dynamics of complex adaptive food webs

by

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Declaration

By submitting this thesis electronically, I declare that the entirety of the work contained therein is my own original work, that I am the authorship owner thereof (unless to the extent explicitly otherwise stated) and that I have not previously, in its entirety or in part, submitted it for obtaining any qualification.

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Abstract

The eco-evolutionary dynamics of complex adaptive food webs

Predator-prey interactions are ubiquitous since almost every species on earth participates in at least one predator-prey interaction. As a result, they shape the food web structure, the functioning of ecosystems and the response to perturbations. Predator-prey interactions have been studied extensively. However, the interplay between their ecological and evolutionary dynamics and how these contribute to regulate food web dynamics have received less attention. In this thesis, therefore, I developed a predator-prey model in which the predator exhibited type II functional response, its body size could evolve and its handling time was dependent on predator-prey body size ratio. Using adaptive dynamics, a mathematical tool which has been developed to study feedback between ecological and evolutionary processes, I investigated the influence of non-linear functional response on the evolution of predator's body size. I found that increasing handling time reduces the predator's body size. In fact, there exists a threshold beyond which an increase in handling time drastically reduces the body size such that evolutionary regime shifts occur. I concluded that predators' feeding rates, as influenced by the current climate trends, coupled with evolution, could explain the observed regime shifts in species body sizes. I extended this model to allow for polymorphism and showed that starting with a single prey and predator, food webs emerge through the process of mutation and natural selection. I checked the density-body size relationship in the emergent food webs to investigate the generality of the energetic equivalence rule and found no support for it. Instead, my results showed a hump-shaped relationship, except for food webs that were generated from the predators which exhibited the linear functional response. I further allowed potential invaders into co-evolving food weds to test how invasion success depends on species body size, propagule pressure, native species diversity and introduction time. I found that whenever potential invaders have a bigger body size, they always have a higher invasion success. In addition, I found that although the propagule pressure plays an important role, it is irrelevant in a diverse food web in which most or all niches have been occupied, hence strongly supporting the diversity-invasibility hypothesis.

Opsomming

'Die eko-evolusionêre dinamika van komplekse adaptiewe netwerke'

Predator - prooi-interaksies is alomtegenwoordig, aangesien byna elke soort op aarde deelneem aan ten minste een roofdier-prooi-interaksie. As gevolg hiervan vorm hulle voedselwebstruktuur, die funksionering van ekosisteme en die reaksie op versteurings. Predator-prooi-interaksies is omvattend bestudeer, maar die wisselwerking tussen hul ekologiese en evolusionêre dinamika en hoe dit bydra tot die regulering van voedselwebdinamika, het minder aandag gekry. In hierdie proefskrif het ons dus 'n roofdier-prooi-model ontwikkel waarin die roofdier tipe II funksioneel vertoon het. Sy liggaamsgrootte kan ontwikkel en die hanteringstyd is afhanklik van die verhouding tussen roofdiere-prooi en die liggaam. Met behulp van adaptiewe dinamika, is 'n wiskundige instrument ontwikkel om terugvoer tussen ekologiese en evolusionêre prosesse te bestudeer. Ons het die invloed van nie-lineêre funksionele reaksie op die evolusie van roofdier se liggaamsgrootte ondersoek. Ons het gevind dat toenemende hanteringstyd die liggaam se grootte van die roofdier verminder. Trouens, daar bestaan 'n drempel waaroor 'n toename in hanteringstyd die liggaamsmassa drasties verminder, sodat evolusionêre regime verskuiwings voorkom. Ons het die gevolgtrekking gekom dat roofvoerders se voedselsyfers soos beïnvloed deur die huidige klimaatneigings, tesame met evolusie, die waargenome regime verskuiwings in spesies liggaamsgroottes kan verduidelik. Ons het hierdie model uitgebrei om polimorfisme moontlik te maak en het getoon dat met die begin van 'n enkele prooi en roofdier, voedselwebs ontstaan deur die proses van mutasie en natuurlike seleksie. Ons het die verhouding tussen digtheid en liggaamsgrootte in die opkomende voedselwebs nagegaan om die algemeenheid van die energetiese ekwivalensiereël te ondersoek en het geen ondersteuning daarvoor gevind nie. In plaas daarvan het ons resultate 'n bultvormige verhouding getoon behalwe vir voedselwebs wat uit die roofdiere gegenereer is wat die lineêre funksionele reaksie vertoon het. Ons het verder potensiële indringers toegelaat om voedselwedings te gebruik om te toets hoe die inval sukses afhang van die grootte van die spesies, propagule druk, inheemse spesies diversiteit en inleidingstyd. Ons het gevind dat wanneer potensiële indringers 'n groter liggaamsgrootte het, hulle altyd 'n hoër inval sukses het. Daarbenewens het ons bevind dat hoewel die propagule druk 'n belangrike rol speel, dit irrelevant is in 'n uiteenlopende voedselweb waarin meeste of alle nisse beset is, en daarom die diversiteit-invasibiliteitshipotese sterk ondersteun.

Dedications

To my family

Acknowledgements

As iron sharpens iron, so one man sharpens another.

Proverbs 27:17

My greatest praise goes to the Almighty God for the energy and courage to complete this thesis. My greatest gratitude goes to Professor Cang Hui, who has been a supervisor full of knowledge, guidance, support, inspiration and above, all patient. Indeed, as iron sharpens iron, Prof. Cang Hui has been very generous in making me what I am with respect to life and research. I am also grateful to Dr. Ulf Dieckmann and Dr. Åke Brännström for constructive comments from the initial stages of this thesis. Great thanks to Henintsoa Onivola Minoarivelo, Pietro Landi and Mihaja Ramanantoanina for the exchange of ideas and inspirations that have contributed a lot to the completion of this thesis.

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List of publications

The following publications were developed during this doctoral dissertation (2013- 2017). However, they are not included as part of this theses' chapters because their main ideas originate from either my Master's thesis or collaborative work.

Nuwagaba, S., Zhang, F. and Hui, C. (2015) A hybrid behavioural rule of adaptation and drift explains the emergent architecture of antagonistic networks. Proceedings of the Royal Society B: Biological Sciences, 282: 20150320.

Nuwagaba, S. and Hui, C. (2015) The architecture of antagonistic networks: Node degree distribution, compartmentalization and nestedness. Computational Ecology and Software, 5: 317-327.

Hui, C., Minoarivelo, H.O., **Nuwagaba, S.** and Ramanantoanina, A. (2015) Adaptive diversification in co-evolutionary systems. In: P. Pontarotti (ed.) Evolutionary Biology: Bio-diversification from Genotype to Phenotype. Springer, Berlin, pp.167-186. ISBN: 978-3-319-19932-0.

Nuwagaba, S., Zhang, F. and Hui, C. (2017) Robustness of rigid and adaptive networks to species loss. Journal of computational ecology, submitted.

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CHAPTER 1

Introduction

"Mathematics is much more than a language for dealing with the physical world. It is a source of models and abstractions which will enable us to obtain amazing new insights into the way in which nature operates. Indeed, the beauty and elegance of the physical laws themselves are only apparent when expressed in the appropriate mathematical framework."

Melvin Schwartz, In Principles of Electrodynamics.

1.1 Background

Biodiversity and human dependency

According to the United Nation's Department of Economic and Social Affairs (2017) world population prospects, approximately 7.6 billion people inhabit the earth (UN-DESA 2017) and so do 9 million types of plants, animals, protists and fungi (Cardenile et al. 2012). The human population is expected to continue growing while plants and animals are declining. This decline in biodiversity is highly anthropogenic because humans have altered ecosystems today more extremely than ever. However, it is important to acknowledge that this alteration has been due to the growing demands for resources (Guo et al. 2010). We are all racing in the struggle for life and following the current economic development, many scientists and the public are concerned about how to quantify ecological services in monetary terms to understand whether we are as dependent on these services as before (de Groot et al. 2012; Guo et al 2010). This has not been easy because most of the ecosystem value is non-tradable; however, this search has served to answer questions regarding why we would be so concerned about biodiversity emergence, conservation and maintenance. In fact, Guo et al. (2012) show that economic growth has made humans more dependent upon ecosystem services and biodiversity than before. Unfortunately, *'the over-exploitation of ecosystems thus comes at the expense of the livelihoods of the poor and future generations'* (de Groot et al. 2012).

It is rather unfortunate that we are just beginning to appreciate the wealth of human health benefits that stem from experiencing nature and biodiversity. These benefits range from water quality regulation, landscape aesthetics, atmospheric regulation, pest regulation, pollination, recreation and more (Harrison et al. 2014). In fact, Sandifer et al. (2015) compiled a comprehensive listing of reported health effects of biodiversity such as reducing certain allergic

and respiratory diseases plus some psychological and physiological benefits. All evidence shows that although nature can do without us, we cannot do without it. Unfortunately, regardless of initiatives like the United Nations 2010 declaration of the decade on biodiversity among others, species continue to decline at both ecological and evolutionary scales and we do not yet understand how to buffer the occurrence. Improving our understanding of at least some of the key processes and relationships that enhance biodiversity conservation will help guide effective management and protection strategies (Harrison et al. 2014).

Predator prey co-evolution

Predator-prey interactions are ubiquitous and a pivotal part of both ecological and evolutionary dynamics in their complex nature. In fact, all animals could be either predators or preys and most of the time, they may be both i.e. they feed on species in lower trophic levels while being fed on by those in higher trophic levels than theirs. In their interactions, the predator could change behaviour or its traits as a result of specific changes in its prey. This is called co-evolution. Darwin, in his book '*The origin of species'*, explained that the species traits such as body size which we see today and their evolution have been shaped by their interactions with other species in a complex but yet well-coordinated manner.

Today, the co-evolution of predators and their preys, following the high human population growth and technological advances, has suffered unique challenges, the most alarming being biodiversity decline (Thomas et al. 2004). In addition, changes in climate have caused alterations in predator-prey interactions at different scales (Codron et al. 2017; Julien et al. 2017; Chiba & Sato 2016; DeGregorio et al. 2015; Lurgi et al. 2012; Thomas et al 2004). Most of these changes seem to root from alteration of predator functional responses, foraging behaviour and body traits and the interactions between them (Spanbauer et al. 2016; Sentis et al. 2013; Kalinkat et al.; 2013, Rall et al.; 2012, Englund et al.; 2011, Smith et al.; 2010,

Thomas et al. 2006; Thomas et al. 2004). As a result, understanding how predator-prey interactions and their specific processes influence the co-evolution of species body sizes, food webs and food web structure could improve our preparedness for this ever-changing environment.

Modelling of co-evolution in food webs

Food webs have more complex dynamics as they contain the variety of interaction types. As a result, unlike simple predator-prey interactions which can be studied in laboratories, food webs are almost impossible to study in a laboratory setting. Nonetheless, mathematical models of co-evolution, among others, such as the cascade, niche and evolution models, have been suggested to understand the emergence of food webs and exploring conditions that foster diversification within and across trophic levels (Hui et al. 2015; Brännström et al., 2012; Brännström et al. 2011; Loeuille & Loreau, 2005; Cattin et al. 2004). For example, Brännström et al. (2011) explored the role of body size in the co-evolutionary dynamics of food webs and in structuring and maintaining food web biodiversity. The standing challenge is that this particularly informative model used the type one functional response which assumes that the number of prey consumed by a predator is directly proportional to the prey density. Such an assumption is only valid when the prey density is very low; otherwise, there is a maximum consumption rate that should be reached due to the gut capacity of any predator. Therefore, it is important to investigate how non-linear functional responses alter the emergence of food webs, their structure and response to anthropogenic disturbances.

Invasion in food webs

The invasion of ecosystems by non-native species has widely been considered one of the greatest threats to biodiversity (Lurgi et al. 2014). One of the most studied invasions is of the

Nile Perch, which was introduced into Uganda's largest fresh water lake, Lake Victoria, in 1969, to control the biomass of the indigenous small bony haplochromine cichlids and to probably improve production in the fishing industry, given the large size of the Nile Perch. Today, the native small bony cichlids have not only reduced but are almost extinct (van Zwieten et al. 2016). Similar happenings have been observed across the globe (Lovett et al. 2016; Blackburn 2014). One of them is the forest pest, Emerald ash borer, *Agrilus planipennis*. It has been labelled the most costly invader in North America because it may take approximately US$12.7 billion to respond to its kind of invasion by 2020 (Lovett et al. 2016). To combat such an expense, in addition to biodiversity loss, we need to understand the properties of invaders and natives that interact to foster the extravagant establishment of these invaders. Although some species traits such as body size and other factors such as the propagule pressure, time of introduction, niche space, etc., have been identified as good predictors of invasion success (Lurgi et al. 2014), a consensus about most of them has not been reached. Moreover, testing some of the commonly debated factors associated with successful invasions in a co-evolving system of interacting species has received less attention.

1.2 Thesis overview

With ecological and evolutionary processes continuously in a feedback loop at their respective time scales, species body sizes evolve towards smaller or larger sizes, each individual trying to maximize their fitness as they struggle for the survival of their genes. In this thesis, I explore how eco-evolutionary dynamics of predator-prey interactions influence the assemblage of species, establishment of density-body-size relationships and the response of species to invasions by non-native individuals. I do this under the umbrella of adaptive dynamics, a powerful mathematical tool recently developed for examining phenotypic evolution and

divergence (Doebeli & Dieckmann 2000). Consequently, this thesis contains four more chapters in addition to this introduction.

Chapter two explores the evolutionary dynamics of a co-evolving predator and a non-evolving prey. A bifurcation analysis of this system is carried out to investigate the contribution of non-linear functional response on the existence of bifurcation points, which could be considered to be regime shifts in the system.

Chapter three extends the model used in Chapter two by allowing polymorphism to happen through mutation and directional selection to investigate the processes that lead to the emergence of food webs, with an interest in how non-linear functional response influence the structure of the emergent food webs. Specifically, this chapter investigates the generality of the energetic equivalence rule, which states that the amount of resource utilised by a species is independent of their body size.

Chapter four introduces potential invasive individuals into the co-evolving food webs produced in Chapter three to understand the factors that enhance the establishment of non-native individuals in a new area. It investigates some of the common invasion hypotheses in the presence of co-evolution in food webs.

Chapter five gives concluding remarks and potential extensions of this work.

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CHAPTER 2

Inefficiency in prey handling jeopardizes the predator's body size.

"The question is, are we happy to suppose that our grandchildren may never be able to see an elephant except in a picture book?"

David Attenborough.

ABATRACT

Predator functional responses and the parameters that define them such as the predator's handling time, greatly influence predator-prey interactions. However, in the advent of rapid evolution due to anthropogenic environmental changes, the role of the handling time on species traits and their evolutionary dynamics has not received due attention. Using a co-evolutionary model, I investigated the impact that a body size dependent handling time has on a system of a co-evolving predator and its autotrophic prey. By carrying out a bifurcation analysis, I found that there is a handling time scalar threshold beyond which a small increase in that scalar results in a drastic decrease in the predator's body size. In addition, phenotypic history seems to enhance the occurrence of the drastic decrease in body size since these shifts were only observed in the presence of evolutionary feedbacks. Therefore, predators' feeding rates as influenced by the current climate trends, coupled with the evolution of functional traits, could explain the observed regime shifts in species body sizes.

Keywords: Predator, prey, co-evolution, handling time, functional response, bifurcation, regime shift, body size.

2.1 Introduction

Predator-prey interactions are at the core of understanding species dynamics within ecosystems. Evidence has shown that anthropogenic disturbances on natural ecosystems have altered the expected dynamics, thus resulting in what is commonly known as "regime shifts" (Gardmark et al. 2015; Rocha et al. 2014; Hughes et al. 2013; Folke et al. 2004; Rose and Harmsen 1981). These are abrupt long-lasting changes in the structure and function of the system and could have drastic implications for human well-being as we heavily depend on

ecosystem functioning and services for food, fuel and fibre. These shifts have been evident in both aquatic and terrestrial ecological systems at both ecological and evolutionary time scales (Folke et al. 2004). In fact, both experimental and theoretical studies have shown that some disturbed systems may exhibit "alternative stable states" (Folke et al.'s (2004) review of regime shifts) which create an uncertainty in forecasting outcomes of any interventions for conservation. Although these alternative steady states have been often identified as purely ecological phenomena, hence occurring over a short period of time, it is prudent to investigate whether a predator-prey system in which predators evolve by natural selection exhibits similar alternative steady states or not as this could inform the long-term impacts of anthropogenic activities on the provisioning services.

Evolution by natural selection often targets species specific traits such as body size whose role in species dynamics is well documented (Cohen et al. 1993). Body size may determine how energy and biomass are proportioned among individuals (Brown 2014), determine whether species co-exist or not (Bowers and Brown 1982) or even limit possible interactions between species (Cattin et al. 2004). It has been believed that species evolve larger body sizes over evolutionary time (Bonner 1988; McLain 1993; Jablonski 1997), thereby enabling them to produce offspring of better quality among other benefits (Clutton-Brock et al. 1982, 1988). This idea has been criticised owing to the fact that it does not provide for assessing the fitness consequences of large body sizes. In their review on the evolution of body size, Blanckenhorn (2000) clearly argued that research biases, possibly motivated by theoretical, practical, and/or economic considerations, have certainly contributed to the lack of studies that investigate viability costs of large body size. In terms of energy requirements, for example, smaller individuals need less energy and can thus reproduce sooner, which supposedly should confer a fitness advantage, as opposed to Cope's rule which stipulates that species lineages tend to increase in body size over evolutionary time. Unfortunately, mechanisms that force selection

toward small body sizes are not clearly understood even though they are crucial for explaining why we are not surrounded by a cloud of gigantic organisms. Moreover, why are some predators smaller than their prey?

One important parameter in understanding predator-prey dynamics is the predator's handling time, which consists of four processes namely: fighting, catching, eating (Holing 1959) and digesting prey items (Jeschke 2002). The predator's efficiency during these processes depends on the body size of the predator relative to that of the prey: for example (i) it is harder for larger predators to catch smaller prey due to constrained locomotor efficiencies since smaller preys are faster at escaping (ii) larger predators take a shorter time to kill and eat prey compared to smaller predators feeding on the same prey and (iii) the time it takes predators to digest their prey is associated with metabolism, whose rate increases with predator's body size (Gillooly et al. 2001). In other words, handling time constrains how much prey a predator is able to consume and process in a given time. It is only natural to anticipate that when handling time is high, the predator is too inefficient in its feeding that it cannot support large body size. In mathematical models, handling time is often captured by the predator functional response, which describes the number of prey a predator consumes as a function of prey density (Holling 1959). The most commonly used functional response is the type II, which shows that the number of prey that a predator consumes increases linearly with prey density at low prey densities, but saturates at high prey densities.

Handling time can further be divided into physical handling time (for fighting, catching and eating) and digestion time (Jeschke et al. 2002), each of which is influenced by temperature. In laboratory experiments in which an aphid parasitoid (*Aphidius colemani*) and one of its common hosts (*Myzus persicae*) were used to examine the effect of temperature on the handling time, Wu et al. (2011) showed that parasitoids reared at 25°C took significantly longer handling times and had smaller body sizes compared to those reared at 15°C. Although their study

implied that handling time increases with temperature, subsequent studies showed that the relationship is rather hump shaped, with maximum handling time observed at intermediate temperatures (Englund et al. 2011; Rall et al. 2012; Sentis et al. 2013). In systems where the digestion time is the dominant component of handling time, it is likely that handling time will, in general, increase with temperature given the dependence of metabolism on temperature otherwise, the hump shaped relationship may arise. In fact, Sentis et al. (2013) concluded that the relationship is confusing and that the interpretation of handling time in mathematical models should be done very carefully since the components of handling time respond differently to temperature. Nonetheless, whether the relationship is linear or hump-shaped, a reliable evaluation of how changes in predator handling time influence predator-prey dynamics and body size evolution is crucial to our understanding of the impact of global warning on the body-size and biomass distribution in our ecosystems.

In this chapter, I use a predator-prey eco-evolutionary model in which the prey is autotrophic to understand the dynamics at both ecological and evolutionary time scales. The model allows for polymorphism but in this chapter, I analyse the predator-prey system before any polymorphism occurs. With several parameters depending on the predator-prey body-size ratio, I use a mathematical tool of adaptive dynamics (Dieckmann and Law 1996) to investigate (1) how the predator's handling time influences body size evolution and population densities and (2) the influence of evolutionary feedback on ecological dynamics. In addition, I use bifurcation analysis to (3) examine the existence of evolutionary thresholds which mark alternative steady states and hence possible evolutionary regime shifts and (4) understand the implications of predator handing time for polymorphism and hence diversification.

2.2 Methods

2.2.1 The Model:

The demographic model is a derivative of the classical predator-prey model consisting of one predator and one prey. I chose the model with a type II functional response owing to the fact that at higher prey densities, the predator can only consume prey relative to its gut size and hence the saturation (figure 2.1).

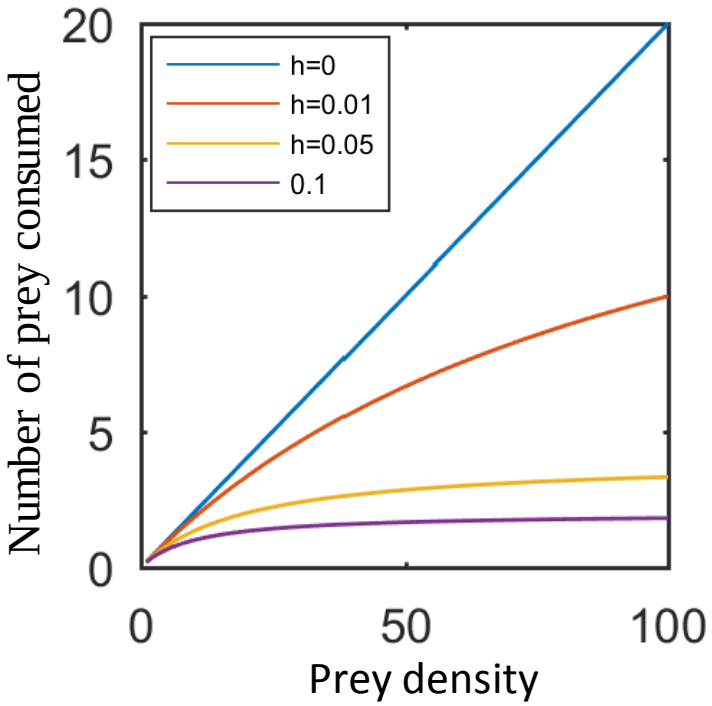

Figure 2.1: The shape of type II functional response. The function used to generate the above figure is: Number of prey consumed = a*Prey density/(1+ h*Prey density), where 'a' is the attack rate.

To incorporate the evolutionary aspect, I used body size as the characteristic adaptive trait to capture feedback between the predator's feeding properties and its body size evolution. Therefore, I consider a basal autotrophic prey with population density n_0 and body size s_0 and

a predator with population density n_1 and body size s_1. To avoid the bias that could arise from using absolute body sizes (Wu et al.2011), I defined the body size of the predator relative to that of the prey hence $x_1 = \ln(s_1/s_0)$. Therefore, demographic dynamics can be described by the following system of equations:

$$\dot{n}_1 = -d(x_1)n_1 - k_1 n_1^{\,2} + \lambda \frac{s_0}{s_1} \frac{\gamma_{10} n_1 n_0}{1 + h_{10}\gamma_{10} n_0} \tag{2.2.1}$$

$$\dot{n}_0 = r n_0 - k_0 n_0^{\,2} - \frac{\gamma_{10} n_1 n_0}{1 + h_{10}\gamma_{10} n_0} \tag{2.2.2}$$

where the intrinsic mortality rate $d(x_1) = d_0 \exp(-qx_1)$ describes the loss of biomass due to respiration hence capturing the allometric scaling of metabolic rate with body mass (Brännström et al. 2011), k_1 defines the strength of intra-specific competition among the predators, λ is the fraction of prey biomass that a predator uses for its reproductive growth while γ_{10} describes the rate of predation and is assumed to follow a normal distribution, that is:

$$\gamma_{10} = \frac{M_\gamma}{\sqrt{2\pi}\sigma_\gamma} \exp\left(\frac{-(x_1 - x_0 - \mu)^2}{2\sigma_\gamma^2} \right)$$

Where M_γ is the amplitude of the consumption kernel, μ defines the predator to prey body size ratio around which the predator realises most successful attacks while σ_γ defines the predator's niche width. h_{10} is the time the predator spends handling one prey. Kalinkat et al. (2013) analysed a data set of arthropods' feeding rates and found that the handling time dependence on predator and prey body sizes follows the function $h_{10} = h_0 s_0 s_1^{-0.75}$ which I adopted for my system. Note that when $h_0 = 0$, the model exhibits Hollings type I functional

response and type II otherwise. r is the growth rate of the prey while k_0 is the strength of density dependence in the prey population.

Evolutionary dynamics arise from the emergence of new traits through the process of mutation. Following the theory of adaptive dynamics, (i) I assume that mutants are rare and that they appear when the demographic dynamics are at equilibrium ($\bar{n}_0, \bar{n}_1$). With the introduction of a rare mutant with relative body size x_1' and density n_1', the system is modified to:

$$\dot{n}_1 = n_1\left(-d(x_1) - k_1 n_1 + \lambda \frac{s_0}{s_1}\frac{\gamma_{10} n_0}{1 + h_{10}\gamma_{10} n_0} - \alpha_{11'} n_1'\right) \tag{2.2.3}$$

$$\dot{n}_1' = n_1'\left(-d(x_1') - k_1 n_1' + \lambda \frac{s_0}{s_1'}\frac{\gamma_{1'0} n_0}{1 + h_{1'0}\gamma_{1'0} n_0} - \alpha_{1'1} n_1\right) \tag{2.2.4}$$

$$\dot{n}_0 = n_0\left(r - k_0 n_0 - \frac{\gamma_{10} n_1}{1 + h_{10}\gamma_{10} n_0} - \frac{\gamma_{1'0} n_1'}{1 + h_{1'0}\gamma_{1'0} n_0}\right), \tag{2.2.5}$$

where α_{ij} describes the mortality rate as a result of interference competition between the resident and mutant predators. Here, I define

$$\alpha_{1'1} = \frac{1}{\sqrt{2\pi}\sigma_k}\exp\left(\frac{-(x_1 - x_1')^2}{2\sigma_k^2}\right)$$

where σ_k is the width of the competition kernel implying that in equations 2.2.1, 2.2.3 and 2.2.4, $k_1 = \alpha_{ii} = 1/\sqrt{2\pi}\sigma$. At this stage, another assumption is made that the density of the mutant trait is so low that it has no effect on the per-capita growth rate. In addition, I assume that the prey does not evolve. I therefore derive the initial per-capita growth rate of the rare mutant, also known as the invasion fitness as:

$$S(\bar{n}_0, \bar{n}_1, 0, x_0, x_1, x_1') = \frac{\dot{n}_1'}{n_1'} = -d(x_1') + \lambda \frac{s_0}{s_1'} \frac{\gamma_{1'0} n_0}{1 + h_{1'0} \gamma_{1'0} n_0} - \alpha_{1'1} n_1 .$$

To describe the rate of change of the relative body size of the predator over evolutionary time, I use the canonical equation of adaptive dynamics given as:

$$\frac{dx_1}{dt} = \varepsilon \frac{\partial S(\bar{n}_0, \bar{n}_1, 0, x_0, x_1, x_1')}{\partial x_1'}\bigg|_{x_1' = x_1}, \tag{2.2.6}$$

where t is the evolutionary time, ε scales the speed of evolutionary change (Dieckmann and Law 1996, Brännström et al. 2013) and $\frac{\partial S(\bar{n}_0, \bar{n}_1, 0, x_0, x_1, x_1')}{\partial x_1'}\Big|_{x_1' = x_1}$ is the slope of the invasion fitness at $x_1' = x_1$, also known as the selection gradient. If the selection gradient is positive (negative), mutants with slightly higher (lower) values may successfully invade. The points at which the selection gradient nullifies are of special interest because at such points, the evolutionary process may come to a halt or polymorphism may arise. This result is determined by the sign of the curvature of the fitness landscape at these points. If the curvature is positive, polymorphism arises through a process called evolutionary branching, otherwise an evolutionary stable strategy (ESS) is reached.

The model above was numerically analysed at ecological and evolutionary time scales to understand the influence of eco-evolutionary feedbacks on the dynamics of the system. I used an ordinary differential equation solver for stiff functions, ODE15s, in MATLAB to solve the system of equations. A numerical bifurcation analysis of the model was also carried out using continuation techniques (a method of computing approximate solutions of a system of parameterised nonlinear equations) with respect to a number of parameters. Algorithms in these techniques take as input a system of parameterised nonlinear equations and an initial solution which they use to produce a set of points on the solution curve. In this chapter, I used a software

called MATCONT (freely available at https://sourceforge.net/projects/matcont/), which implements a prediction-correction continuation algorithm based on the Moore-Penrose matrix pseudo-inverse (Dhooge and Govaerts 2003).

2.2.2 Numerical simulations

Each numerical simulation started with the population density of 1 for both the prey and the predator. The logarithm of the trait value (relative body size) of the predator was initially at 3 while that of the prey autotrophic prey was at 0. To separate ecological and evolutionary dynamics, the parameter ε in equation 2.2.6 was set to 0.03. Once population dynamics reached equilibrium, the conditions for evolutionary branching, according to adaptive dynamics theory, were tested to check for the possibility of polymorphism. In all cases, I carried out tests for different values of the handling time scalar h_0. In the case of numerical continuation, the initial conditions were the same as in the above simulation while using MATCONT software. Other parameter values are indicated in figure captions.

2.3 Results

While increasing the predator's handling time scalar (sometimes lightly called handling time) in my evolutionary predator-prey model simulations, the body size of the predator reduced. In fact, simulations showed that there exists a threshold beyond which a small increase in handling time scalar results in a drastic decrease in the predator's body size to the extent that it gets smaller than that of its prey (Fig 2.2a). In addition, there is a drastic change in the population density equilibrium corresponding to the drastic change in body size (Fig 2.2b). This kind of a drastic decrease could be looked at as an evolutionary regime shift in body size. Moreover, a

bifurcation analysis of the model revealed areas of bi-stability for non-linear functional responses ($h_0 \neq 0$). These are regions in which the system exhibits alternative steady states. This was evident through the detection of two saddle node bifurcation points during the model bifurcation analysis with respect to the width of the consumption kernel (niche width), σ_γ, the width of the competition kernel (inverse of the strength of competition), σ_k and conversion efficiency (fraction of consumed prey that a predator uses for reproduction), λ (Fig 2.3). Although these tipping points were not detected with respect to the prey growth rate (Fig 2.3d), drastic reductions in body size are evident as the non-linearity (handling time) is increased.

It is important to note that for low handling time in all cases, there was a steady decrease in body size but no tipping points. In cases where tipping points were not detected, the slope of the smooth decrease, in relative body size of the predator with respect to the parameters, was either approximately equal to or higher than when $h_0 = 0$ (Figure 2.3b). In fact, the equilibrium curve for type I functional response ($h_0 = 0$) was the boundary for the other equilibrium curves in the relative body size-parameter plane, emphasising that the increase in non-linearity of the functional response increased the chances of evolutionary regime shifts.

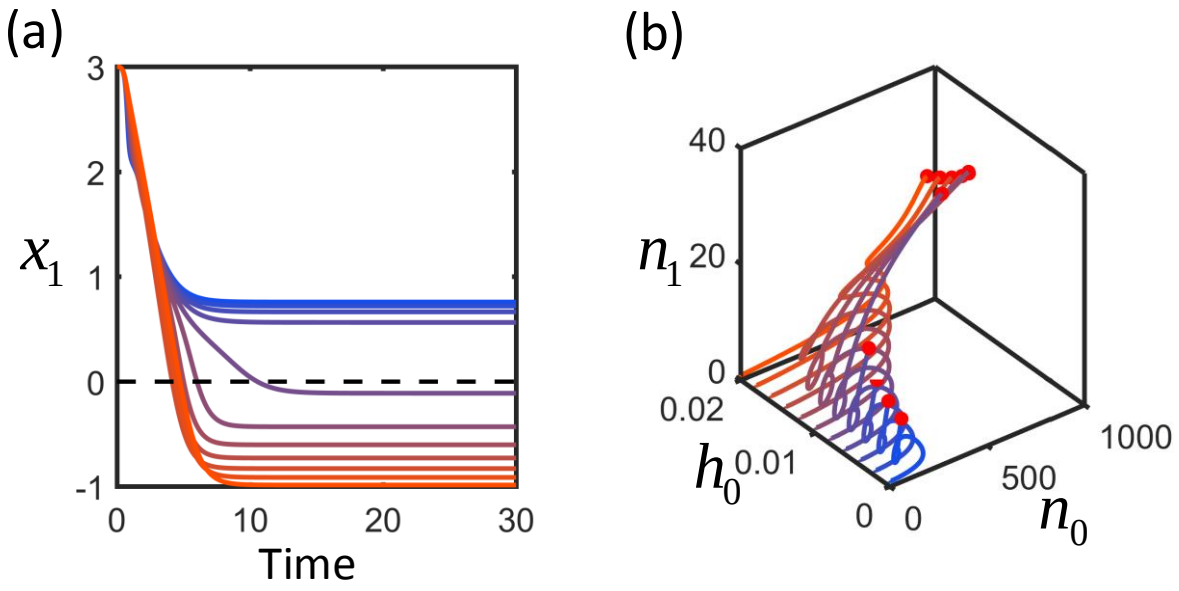

Figure 2.2: Changes in the predator's body size and population equilibrium for different handling times. Panel (a) shows the time series of the predator's body size as handling time changes while (b) shows how the equilibrium points change as handling time changes. n_1, x_1 and h_0 indicate the predator's density, relative body size and handling time scalar, respectively, while n_0 is the prey's density. With different values of h_0, all simulations were run using parameter values, k_0 = 0.01, d_0 = 0.1, μ = 3, M_γ = 10, σ_γ = 1.5, λ = 0.3, q = 0.25, σ_k = 0.6, r = 10, s_0 = 1. The dotted line in panel (a) indicates the zero line (body size of the predator equals that of its prey). The colour code indicates the value of h_0, where blue is the lowest and red the highest.

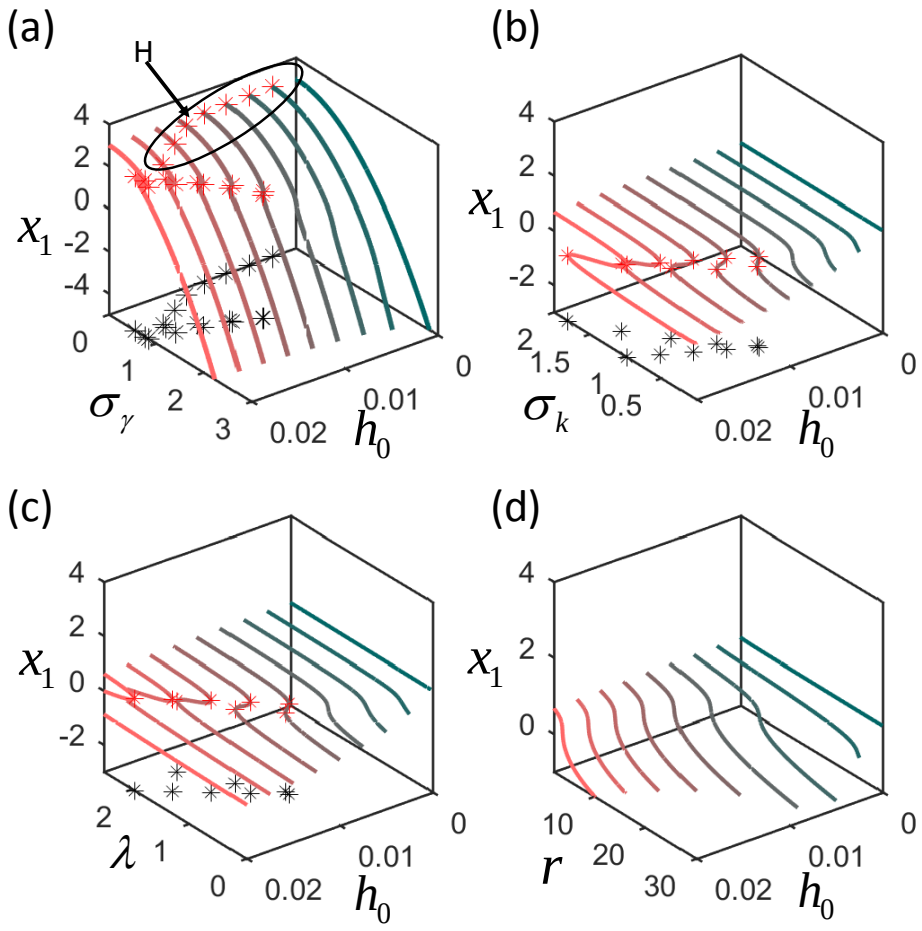

Figure 2.3: Changes in body size at equilibrium as different parameter values change. For different values of the handling time scalar (h_0), panels (a), (b), (c), and (d) show continuation curves (interpreted as changes in the predator's body size at equilibrium) with respect to the standard deviation of the consumption kernel (σ_γ), standard deviation of the competition kernel (σ_k), heterotroph's conversion efficiency (λ) and autotroph intrinsic birth rate (r) gradients, respectively. Each continuation curve corresponds to a different value of the handling time scalar where red indicates the highest handling time. x_1 indicates the predator's relative body size while the stars, except the ones labelled 'H', indicate the saddle node bifurcation points. Stars labelled 'H' indicate the Hopf bifurcation points. Other parameter values were, $k_0 = 0.01$, $d_0 = 0.1$, $\mu = 3$, $M_\gamma = 10$, $\sigma_\gamma = 1.5$, $\lambda = 0.3$, $q = 0.25$, $\sigma_k = 0.6$, $r = 10$, $s_0 = 1$.

Simulations also showed that with an increase in the predator's handling time, evolutionary feedback had a stronger influence on population densities than ecological feedback. Ecological thresholds which were observed during simulations with body size evolution did not arise when evolution was not allowed (Fig 2.4). Results showed that after a certain h_0 threshold, the drastic changes in the time series of the density of the predator that included evolutionary feedbacks differed significantly from the ones during which evolution was excluded (Fig 2.4a vs 2.4b). Figure 2.4 shows that when h_0 was increased, the densities of both the predator and the prey at equilibrium increased. This increase was persistent without evolutionary feedbacks (Figure 2.4a and 2.4c). In simulations that included evolution, there was a threshold after which an increase in h_0 decreased the density of the predator at equilibrium (Figure 2.4b). Although the density of the prey increased with increasing handling time with or without the predator's evolution, the sharp increase was also observed during evolution, thus indicating the obvious effect of the predator's evolutionary dynamics on the prey's population density.

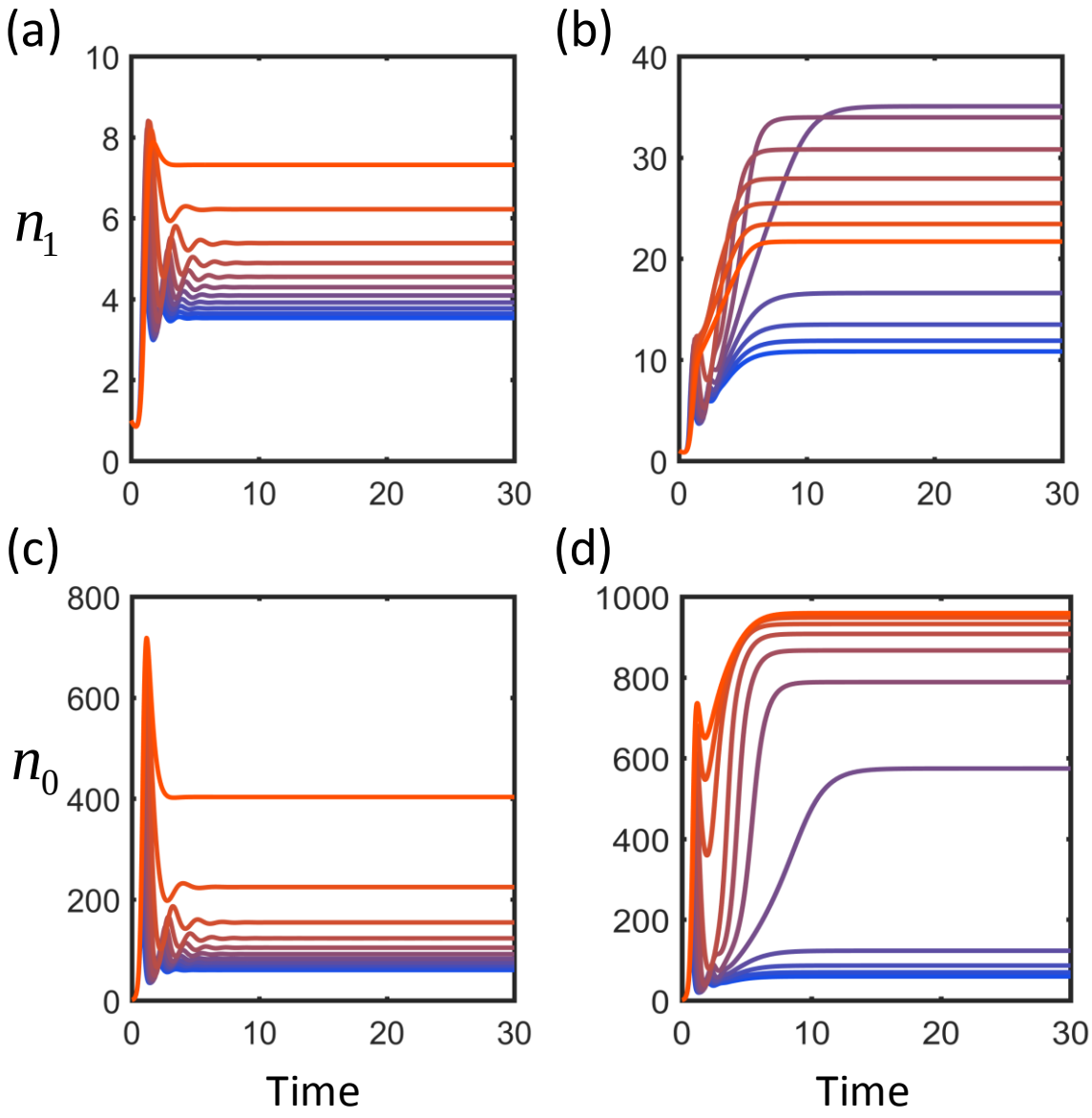

Figure 2.4 Time series of the prey's and predator's density with and without evolutionary dynamics. Panels (a) and (b) correspond to time series of the predator's population density with and without evolution while panels (c) and (d) show respective time series for the prey population density. Different trajectories correspond to different handling time scalars, h_0, increasing from blue to red. n_1 and n_0 indicate predator and prey density, respectively. With different values of h_0, all simulations were run using parameter values, $k_0 = 0.01$, $d_0 = 0.1$, $\mu = 3$, $M_\gamma = 10$, $\sigma_\gamma = 1.5$, $\lambda = 0.3$, $q = 0.25$, $\sigma_k = 0.6$, $r = 10$, $s_0 = 1$.

I quantified the strength of disruptive selection as the curvature of the selection gradient and found that an increase in the handling time increases the strength of disruptive selection hence the possibility of biodiversity enhancement but only up to a threshold. Figure 2.5a shows that the strength of disruptive selection increased to a threshold beyond which it drastically increased and shortly started to decrease. This indicated that biodiversity is maximum when a predator's handling time is intermediate rather than very high or low. Importantly, this drastic decrease in disruptive selection happened at the same values of handling time scalar at which there was a drastic change in the density of the predator. I also noted that the competition influenced disruption more than predation did (Fig 2.5b). In fact, while competition enhanced disruption, predation served to stabilise the system against disruptive selection pressures.

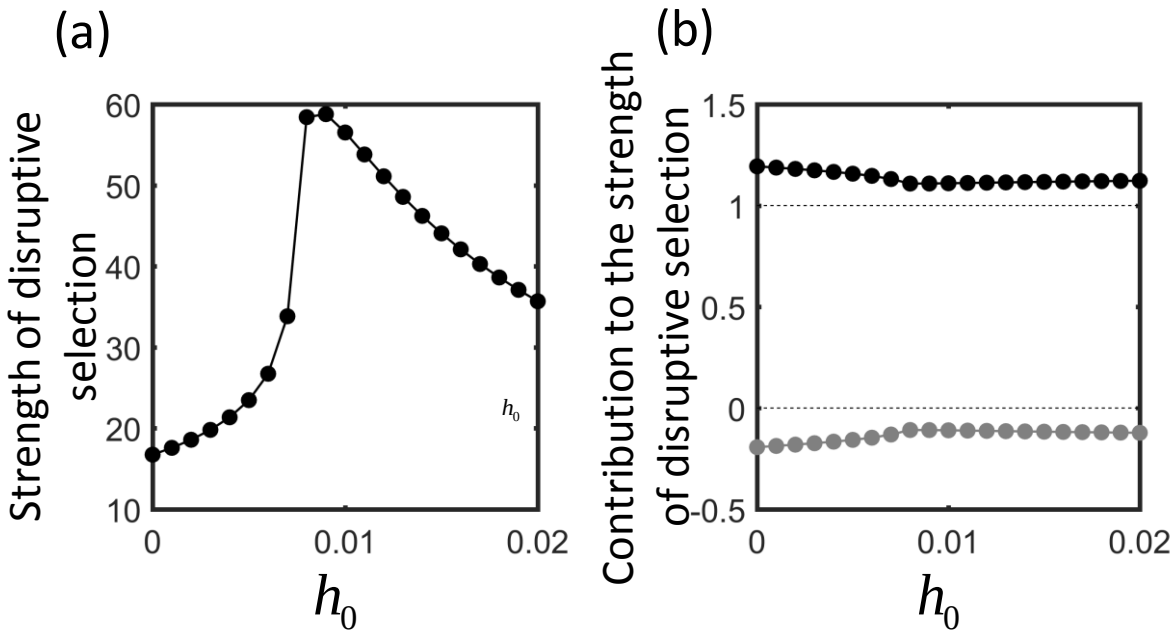

Figure 2.5: Variation in the strength of disruptive selection with handling time. Panel (a) shows how handling time affects the strength of disruptive selection while panel (b) shows the relative contribution of competition and predation to the strength of disruptive selection. Other parameters were: $k_0 = 0.01$, $d_0 = 0.1$, $\mu = 3$, $M_\gamma = 10$, $\sigma_\gamma = 1.5$, $\lambda = 0.3$, $q = 0.25$, $\sigma_k = 0.6$, $r = 10$, $s_0 = 1$.

2.4 Discussion

Body-size mediated effects on predator-prey dynamics have been well documented by both experimental and theoretical ecologists (Brown 2014; Bowers and Brown 1982; Cattin et al. 2004; MacNulty et al. 2009; Cohen et al.1993). In their analysis of a data set of arthropod feeding rates, Kalinkat et al. (2013) showed that all functional response parameters depended on body size. However, it has been pointed out that some of these dependencies should be to relative rather than absolute species' body sizes (Wu et al. 2011). For instance, Wu et al. (2011) conducted an experiment whose results revealed that the handling time increased with prey size

for small predators but not for the large ones; supporting the notion that to consider the handling time dependence on body size, one must use the predator-prey body size ratio rather than absolute body size. This justifies the fact that in my eco-evolutionary model, the parameters depended on relative rather than absolute body sizes.

Results from the model showed that as the handling time increases, the density of the predator increases up to a certain threshold beyond which it decreases (Fig 2.4b). An increase in handling time can literally mean that a predator spends a long time processing one prey item. As a consequence, the prey population grows high, and the predator has plenty of resource. However, this under-utilisation leads to strong competition among the preys which eventually exclude each other and become insufficient for the predator. My results corroborate with Schreiber and Vejdani (2006). I agree that the correlation between predator and prey abundance depends on handling time in such a way that for short handling times, the relationship is negative and positive otherwise, supporting an inverse per-capita predator density relationship for high handling time.

In 2009, Pelletier and colleagues concluded that nothing in evolution or ecology makes sense except in light of the other. Inherently, adaptive dynamics approach, which I used to study my co-evolutionary model, was devised to account for feedbacks between ecological and evolutionary processes. These feedback loops are ubiquitous. Using a chemostat experiment, Becks et al. (2012) compared the relative importance of ecological and evolutionary effects day-by-day for each chemo run and found that they fluctuated often in opposite directions and that the overall effect of evolution on the growth rate was, in all cases, equal to or higher than the ecological one. These evolutionary changes are mainly driven by natural selection which depends on the phenotypic and ecological state of a population. I argue that viewing ecological systems in light of their evolutionary histories is paramount to conservation. My model

revealed that in the absence of the predator's body size evolution, the impact of the predator's handling time on population densities can be underestimated (Fig 2.4).

Although some scholars have argued that the primary driver of evolution of giant mammals was diversification to fill ecological niches, others have argued that temperature has constrained the maximum size achieved (Smith et al. 2010). In fact, Smith et al. (2010) continued to argue that the largest mammals evolved when the earth was cooler. Unfortunately, this controversy has not been resolved as recent studies have still not agreed as to whether an increase in temperature elongates the time it takes predators to process their food items or not (Wu et al. 2011; Englund et al. 2011; Rall et al. 2012; Sentis et al. 2013). This makes it unrealistic to make conclusions regarding the effect of the temperature increase on the individual's body sizes.

However, for species such as *Coleomegilla maculata lengi* whose main component of handling time is digestion time (Sentis et al. 2013), one would expect that an increase in temperature will increase handling time and hence drive selection towards small body size, and this result may not be an exception since most predators handle prey faster than they digest them (Jeschke et al. 2002). No wonder that coupled with an increase in handling time, regime shifts in body size occur with changes in niche width, intraspecific competition and the predator efficiency in converting its food into energy or biomass (Fig 2.3a, b and c). In addition, there were drastic decreases in the predator's body size with variation in the initial growth rate of the prey even though no tipping points were detected (Fig 2.3d). Therefore, anthropogenic activities that induce low temperatures could potentially prevent some undesirable regime shifts or at least enhance the reversibility of those that have already occurred.

As biodiversity increase and maintenance are at the heart of ecology, I tracked the possibility of diversification by investigating the possibility of polymorphism at the first evolutionary

singularity. Results showed that the strength of disruptive selection increased with handling time up to a certain threshold beyond which it decreased. This potentially suggests that diversification is favoured by intermediate handling times rather than very low or very high handling times. Considering that handling time increases with temperature among most species, these results could have strong implication for the current climate change debate. In some ranges, increasing handling time could increase biodiversity yet in others, the trend could be opposite (Fig 2.5). In fact, Figueorido et al. (2012) showed that some fauna could diversify due to cooler conditions (intermediate handling times) but fall due to lower absolute values (extremely low handling times). This could also imply that there is no specific trend that fits all species in terms of their response to climate change. Depending on how their functional response changes with temperature, some species could diversify while others could go extinct because of warming. Also, I noticed that the competition term contributes the most to the strength of disruptive selection consistent with previous literature (Brannstrom et al., 2011). Interestingly, predation terms serve to stabilise the system through their negative contribution to the strength of disruption.

My results may have important implications for aquaculture and biological control measures in agriculture. Although the handling time in the natural environment may not be easily influenced, the handling time in mass production of biological control species or in aquaculture could be controlled by variations in temperature. I showed that depending on the ecosystem state, small changes in parameters such as handling time or niche width could result in abrupt irreversible changes in the system affecting body size of the species (which could be biological control species). To better understand the potential impacts of climate change, especially with regard to the warming that our planet is experiencing, we cannot afford to leave non-linear functional responses out of our models, otherwise we risk misguiding management should regime shifts arise. My work also highlights possible research questions regarding how non-

linear functional response could influence the invasion success of a species, whether community properties such as the energetic equivalence rule would still hold in a system that exhibits alternative steady states or how the system would behave if both the predator and the prey could evolve.

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CHAPTER 3

Predator saturation effect enhances food web biodiversity but violates the energetic equivalence rule

"One general law, leading to the advancement of all organic beings, namely, multiply, vary, let the strongest live and the weakest die"

Charles Darwin, The Origin of Species

ABSTRACT

Biodiversity sustains humanity, yet its emergence is still not well understood. In his seminal book *on the Origin of species*, Darwin stated that individuals have a common ancestry**,** and biodiversity increases through mutations due to natural selection. I developed a mathematical model of co-evolution to study the emergence of food webs while varying a predator's functional response. I found that non-linear functional response enhances biodiversity in food webs. Specifically, increasing the predator's handling time did not only increase the diversity in the individuals' body sizes but also introduced both smaller and larger individuals than the smallest and largest in the previous food web respectively. In addition, when I tested the density-body size relationships of the emergent food webs, I found no support for the energetic equivalent rule except in cases where the predator exhibited type I functional response. In fact, for food webs where predators had non-linear functional responses, the relationship was hump shaped, thereby questioning the generality of the energetic equivalence rule.

Keywords: Biodiversity, handling time, functional response, evolution, energetic equivalence rule, body size.

3.1 Introduction

The United Nations declared the years 2011-2020 as their decade on biodiversity (Costanza et al. 2014). Species and biodiversity are important because the survival of humanity almost entirely depends of them. As a result, biodiversity loss can cause tremendous challenges such as a reduction in food supply or reduction in the ability of terrestrial ecosystems to fix anthropogenic carbon-dioxide (Naeem et al. 1994). Understanding how the number of species builds up and how an ecosystem sustains itself is key to a true synthesis of how biodiversity interacts with ecosystem functioning amidst the ever-increasing anthropogenic disturbances. I

argue that biodiversity emergence in a food-web is strongly influenced by the time it takes each predator to process its food - called handling time.

To date, body size seems to be one of the most fundamental traits of an organism across many disciplines such as macro-ecology, life history evolution and horticulture among others. It influences the metabolic rate (Hemmingsen, 1960), growth rate, mortality rate (Peters 1983), foraging rate (Modica et al. 2013; Mittelbach, 1981) to mention but a few. From their analysis of a data set of arthropod feeding rates, Kalinkat et al. (2013) showed that all functional response parameters, one of which is handling time, depend on body size. Anthropogenic disturbances, among other disturbances, have led to the selection for smaller body sizes as a defence mechanism against predators or exploitation.

Under such circumstances, much energy is invested into reproduction, hence increasing population density as opposed to body-mass building. For example, intense fishing in the Atlantic Ocean resulted in the Atlantic code, thus evolving earlier maturation and smaller body size (Schoener, 2011). Owing to the significance of species' body size, its implications for the understanding of the emergence and maintenance of biodiversity and food web structure has been increasingly studied. Brose et al. (2006) showed that about 20% of predators have preys that are larger than they are. I believe that the presence of such predators could have important implications for the density-body size relationship in ecological communities.

Studies on the population density vs body-size relationships have had the energetic equivalence rule (EER) as the benchmark for the findings. The EER predicts that the energy used by different species should be independent of their body size (B). This is because the energy (E) used is assumed to be the product of the density (D) and metabolism (M) i.e. $E \propto DM$, where metabolism, $M \propto B^{0.75}$. For the EER to hold, $D \propto B^{-0.75}$ is such that $E \propto DM = B^{-0.75}B^{0.75} = B^{0}$. However, data and theoretical studies have shown contradicting results (Loeuille and

Loreau 2006; Arneberg et al. 1998; Lawton, 1990; Brown and Maurer 1986). Earlier studies that investigated the density-body size relationship found the exponent close to -0.75 (Damuth 1981). Following the speculation that the EER may emerge from macro-evolution of co-evolving species, Loeuille and Loreau (2006) developed a model of co-evolution. They showed that the population density of species in the emergent food webs decreased with their body size following a power law whose exponent is variable, thus contradicting the EER.

Although many studies have also found varying or different exponents (between -0.73 and -1.05), some have found a completely different density-body size relationship. In the case of parasitic nematodes, Arneberg et al. (1998) found a slope of -0.2, which was far from expected. Lawton (1990) found that although the density generally decreases with body size, there is a small region where the density increases with body size. Such findings have led to strong criticisms of the EER from both the theoretical and empirical views. Obviously, the loss of nutrients as they get transported from one trophic level to another may lead to a sharp decrease in density from the bottom to the top of the food web. However, depending on whether the trophic levels are obviously distinct or not, the sharpness of the decrease in density may vary. Moreover, different exponents have been reported for birds, mammals, aquatic species etc. (Brown and West 2000). Although the processes shaping this relationship are still unclear, they must be partly connected to foraging behaviour and the costs involved for every foraging strategy.

Brannstronme et al. (2011) modified Loeuille's model by including gradual evolution, evolutionary branching and trophic interactions, all of which depended on relative rather than absolute differences in body size. However, the aforementioned studies had an underlying assumption that the rate at which predators encounter and attach their prey is limited by their ability to find the prey. On the contrary, we know that at higher prey densities, the encounter rate of predators with prey saturates. Although some studies have shown that using type I or

type II functional responses makes no difference, many have refuted the idea. For example, adding the handling time to a simple L-V model switches a neutrally stable equilibrium to a globally unstable one while longer handling times weaken the positive correlation between per-capita predation rates and prey density and promote stability under specific conditions (Schreiber and Vejdani 2006). Moreover, in Chapter 2, I showed that non-linear functional response triggers regime shifts which would otherwise not occur.

An important but often ignored behaviour which could affect the functional response among many predators is cannibalism. In 1975, Fox published a review in which he argued that a large proportion of cannibalistic behaviour was observed among terrestrial herbivores. Among insects, it was observed even in the presence of abundant food. Although some studies have reported cannibalism as an experimental artefact or just minor (see review by Fox et al.1975), others have showed that cannibalism increases growth rate of the cannibal and eventually increase its body size at maturity (Claessen et al. 2000; Manica et al. 2002). In the aforementioned model by Brännström et al. (2011), cannibalism was included although its contribution to evolutionary dynamics was not explicitly investigated.

Here, I modify the model in Chapter 2 by allowing cannibalism among consumers and use it to investigate (i) the implications of cannibalism in predator-prey co-evolutionary dynamics (ii) the implication of predator saturation for biodiversity in food webs and (iii) whether the density-size relationship in emergent food webs agrees with the Energetic Equivalence Rule.

3.2 Methods

3.2.1 Predator-prey model

First, I modify the predator-prey model in Chapter 2 to include cannibalism described by the third term in equation 3.2.1 below. The parameter β was added to define the percentage of cannibalistic behaviour in the system. Then the population dynamics model presented in equations 2.2.1 and 2.2.2 of Chapter 2 becomes:

$$\dot{n}_1 = -d(x_1)n_1 - k_1 n_1^{\,2} + \frac{\beta(\lambda-1)\gamma_{11}n_1^{\,2}}{1+h_{11}\gamma_{11}n_1+h_{10}\gamma_{10}n_0} + \lambda\frac{s_0}{s_1}\frac{\gamma_{10}n_1n_0}{1+h_{11}\gamma_{11}n_1+h_{10}\gamma_{10}n_0} \qquad (3.2.1)$$

$$\dot{n}_0 = rn_0 - k_0 n_0^{\,2} - \frac{\gamma_{10}n_1n_0}{1+h_{11}\gamma_{11}n_1+h_{10}\gamma_{10}n_0}$$

All the parameters are as in section 2.2 in Chapter 2. When the model is modified to introduce a rare mutant, equations 2.2.3, 2.2.4 and 2.2.5 become:

$$\dot{n}_1 = n_1\Bigg[-d(x_1)-k_1n_1+\frac{\beta(\lambda-1)\gamma_{11}n_1}{1+h_{11}\gamma_{11}n_1+h_{10}\gamma_{10}n_0+h_{11'}\gamma_{11'}n_1'}$$

$$+\lambda\frac{s_0}{s_1}\frac{\gamma_{10}n_0}{1+h_{11}\gamma_{11}n_1+h_{10}\gamma_{10}n_0+h_{11'}\gamma_{11'}n_1'}$$

$$+\lambda\frac{s_0}{s_1'}\frac{\gamma_{11'}n_1'}{1+h_{11}\gamma_{11}n_1+h_{10}\gamma_{10}n_0+h_{11'}\gamma_{11'}n_1'}-\alpha_{11'}n_1'\Bigg]$$

$$\dot{n}_1' = n_1'\Bigg[-d(x_1')-k_1n_1'+\frac{\beta(\lambda-1)\gamma_{1'1'}n_1'}{1+h_{1'1'}\gamma_{1'1'}n_1'+h_{1'1}\gamma_{1'1}n_1+h_{1'0}\gamma_{1'0}n_0}$$

$$+\lambda\frac{s_0}{s_1'}\frac{\gamma_{1'0}n_0}{1+h_{1'1'}\gamma_{1'1'}n_1'+h_{1'1}\gamma_{1'1}n_1+h_{1'0}\gamma_{1'0}n_0}$$

$$+\lambda\frac{s_0}{s_1'}\frac{\gamma_{1'1}n_1}{1+h_{1'1'}\gamma_{1'1'}n_1'+h_{1'1}\gamma_{1'1}n_1+h_{1'0}\gamma_{1'0}n_0}-\alpha_{1'1}n_1\Bigg]$$

$$\dot{n}_0 = n_0\Bigg[r-k_0n_0-\frac{\gamma_{10}n_1}{1+h_{11}\gamma_{11}n_1+h_{10}\gamma_{10}n_0+h_{11'}\gamma_{11'}n_1'}$$

$$-\frac{\gamma_{1'0}n_1'}{1+h_{1'1}\gamma_{1'1}n_1+h_{1'0}\gamma_{1'0}n_0+h_{1'1'}\gamma_{1'1'}n_1'}\Bigg].$$

Numerical solutions of the predator-prey model in this section were computed as in section 2.2.2 of Chapter 2. In other words, each numerical simulation started with the population density of 1 for both the prey and the predator. The logarithm of the trait value (relative body size) of the predator was initially at 3 while that of the prey autotrophic prey was at 0. To separate ecological and evolutionary dynamics, the parameter ε was set to 0.03. Once population dynamics reached equilibrium, the conditions for evolutionary branching, according to adaptive dynamics theory, were tested to check for the possibility of polymorphism. In all cases, I carried out tests for different values of the handling time scalar h_0. In the case of numerical continuation, the initial conditions were the same as in the above simulation while using MATCONT software.

3.2.2 Food web model

The food web model is an extension of the predator-prey model in section 3.2.1 allowing polymorphism to occur hence food web emergence. Consider a basal autotrophic resource ($i = 0$) and p heterotrophic morphs with population densities ($n_i; i = 1,2,..., p$) such that each morph is associated with a value s_i (interpreted as its average mass). While defining the trait value (relative body size) of each morph as $x_i = \ln(s_i / s_0)$, as in Chapter 2, the dynamics of the heterotrophic morphs can be described by the following equations:

$$\dot{n}_i = -d(x_i)n_i + \sum_{j=0}^{p} \lambda \frac{s_j}{s_i} F_{ij}(\vec{n}, \vec{x})n_i - \sum_{j=1}^{p} F_{ji}(\vec{n}, \vec{x})n_j - \sum_{j=1}^{p} M_\alpha \alpha_{ij} n_i n_j, \qquad (3.2)$$

where the intrinsic growth rate $d(x_i) = \exp(-qx_i)$ (see section 2.2) and λ is the fraction of resource biomass that a consumer uses for its reproductive growth. F_{ij}, also known as the

functional response, is the number of individuals of morph j that are consumed by an individual of morph i as a function of the density of morph j. This function F_{ij} can take a number of forms depending on the processes underlying its divergence from the proportionality principle. α_{ij}, on the other hand, describes the mortality rate as a result of interference competition between morphs i and j while M_α defines the intensity of competition. I define the competition kernel as:

$$\alpha_{ij} = \frac{1}{\sqrt{2\pi}\sigma_k}\exp\left(\frac{-(x_i - x_j)^2}{2\sigma_k^2}\right)$$

such that the closer the body sizes of individuals i and j, the more intense the competition between them. To investigate the role of predator saturation effect in food-web emergence, I consider Holling's type II functional response of the form.

$$F_{ij} = \frac{M_\gamma \gamma_{ij} n_j}{1 + \sum_{k=0}^{n} h_{ik} M_\gamma \gamma_{ik} n_k}$$

where $M_\gamma n_j$ depicts the consumer's encounter rate of individuals of morph j while γ_{ij} describes the probability of a success once a consumer i encounters a resource j and is assumed to follow a normal distribution, that is:

$$\gamma_{ij} = \frac{1}{\sqrt{2\pi}\sigma_\gamma}\exp\left(\frac{-(x_i - x_j - \mu)^2}{2\sigma_\gamma^2}\right)$$

where μ defines the consumer to resource body size ratio around which the consumer realises most successful attacks while σ_γ defines the consumer's niche width. h_{ik} is the time a consumer i spends handling one individual resource k and I define it as $h_{ik} = h_0 s_k s_i^{-0.75}$ (see section 2.2, Kalinkat et al. 2013). The functional response above emerges from the fact that the consumer does not have limitless appetite but rather reduces its marginal intake rate of a resource as the resource density gets overwhelmingly large (Fig 2.1).

The demographic dynamics of the autotrophic resource are described by the equation:

$$\dot{n}_0 = rn_0 - \sum_{j=1}^{p} F_{j0}(\vec{n}, \vec{x})n_j - k_0 n_0^2$$

where r is the growth rate of the resource while k_0 is the strength of density dependence in the resource.

3.2.3 Evolutionary dynamics

Following the theory of adaptive dynamics as explained in Chapter 2, I assume that mutants are rare and appear when the demographic dynamics are at equilibrium. One can then derive the invasion fitness, $S_x(m)$ of a rare mutant with trait value m in an environment dominated by a resident population with the trait values $x_i; i = 1,..., p$. As known, the invasion fitness quantifies the initial growth rate of this rare mutant in an environment set by the residents and can be viewed as the fitness landscape that this mutant experiences. I use the canonical equation of adaptive dynamics to describe the rate of change of trait values over time. This equation takes the form:

$$\frac{dx}{dt} = \varepsilon \left. \frac{\partial S_x(m)}{\partial m} \right|_{m=x},$$

where t is the evolutionary time, ε scales the rate of evolutionary change (Dieckmann and Law 1996, Brännström et al.2013) and $\left. \frac{\partial S_x(m)}{\partial m} \right|_{m=x}$ is the slope of the invasion fitness when $m = r$, also known as the selection gradient. If the selection gradient is positive (negative), mutants with slightly higher (lower) values may successfully invade. The points at which the selection gradient nullifies are of special interest because at such points, the evolutionary process may come to a halt or the diversity of morphs may increase. This result is determined by the sign of the curvature of the fitness landscape at these points. If the curvature is positive,

the diversity of morphs increases through a process called evolutionary branching otherwise, an evolutionary stable strategy (ESS) is reached.

3.2.4 Numerical simulations

Each numerical simulation started with the population density of 1 for both the prey and the predator. The logarithm of the trait value (relative body size) of the predator was initially at 3 while that of the prey autotrophic prey was at 0. To separate ecological and evolutionary dynamics, ε was set to 0.03. Once population dynamics reached equilibrium, the conditions for evolutionary branching according to adaptive dynamics theory in section 3.2.3 above were tested to check for the possibility of polymorphism. The simulations were run until the system reached an ESS.

I tracked the population density, the relative body size and the number of morphs/individuals that emerged when evolution came to a halt. I, therefore, were able to build food webs by computing how much each morph consumed from the other. Prey from which the predator gained less than 10^{-6}, as computed from the functional response, were not considered as part of its diet. For each emergent food web, I quantified biomass of each morph as density x body size ($n_i \times \exp(x_i)$). In all cases, I was able to examine the density-body size relationship for different values of the handling time scalar. I used the least squares method to quantify the exponents of the power law fit to the data.

3.3 Results

3.3.1 Cannibalism and its contribution to predator-prey co-evolutionary dynamics.

To examine the influence of evolutionary feedback on ecological dynamics in the presence of cannibalism, I compared the time series of the population density of the heterotrophic morphs

with different values of the handling time parameter - when body size evolution was considered to when it was not considered as in Chapter 2. Results did not differ much from what was observed without cannibalism. I showed that after a certain h_0 threshold, the time series of the density of the heterotroph that included evolutionary feedbacks differed significantly from the ones during which evolution was excluded.

Figures 3.1(a), (b) and (c) show that when h_0 was increased, the density of the heterotrophic morph at equilibrium increased. This increase was persistent without evolutionary feedbacks (Fig 3.1 (b)). In simulations that included evolution, there was a threshold after which an increase in h_0 decreased the density of the heterotrophic morph at equilibrium (Figure 3.1(c)). However, regardless of the changes in the densities, the relative body size of the heterotroph consistently decreased with an increase in h_0 (figure 3.1(d)). For certain values of h_0, the relative body size of the heterotroph at equilibrium was below the 'zero line', which indicated the existence of consumers that are smaller than their resource.

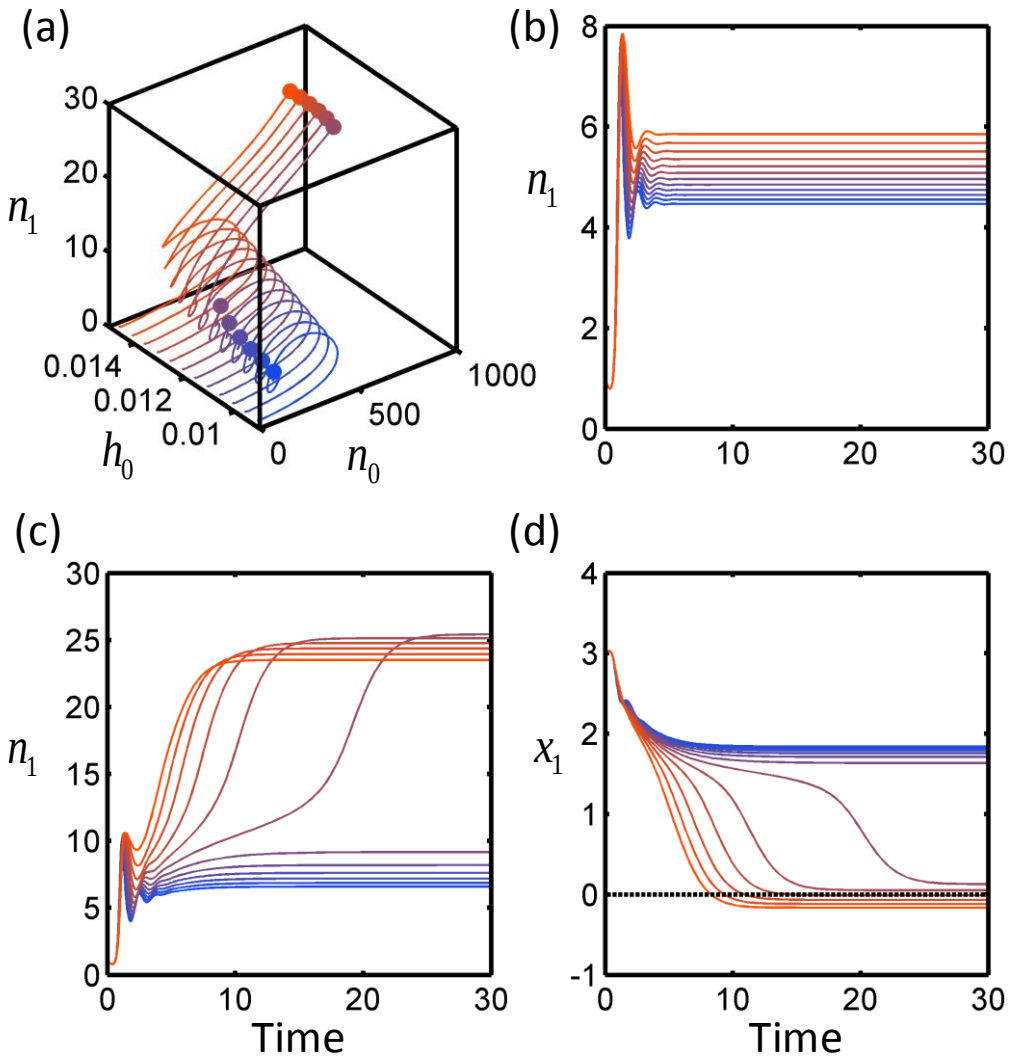

Figure 3.1: Changes in population densities with and without evolutionary feedback. n_1, x_1 and h_0 indicate heterotroph density, heterotroph's relative body size and handling time scalar, respectively. With different values of h_0, all simulations were run using parameter values, k_0 = 0.01, d_0 = 0.1, μ = 3, M_γ = 10, σ_γ = 1.5, λ = 0.3, q = 0.25, M_k = 1, σ_k = 0.6, r = 10, s_0 = 1. Panels (a), (c) and (d) include both evolutionary and ecological feedbacks while panel (b) does not include evolutionary feedbacks. Dots in panel (a) indicate the evolutionary singular points at the first branching point for various values of h_0 while the dotted line in panel (d) indicates the zero line (relative body size of the autotroph). The colour code indicates the value of h_0, where blue is the lowest and red the highest.

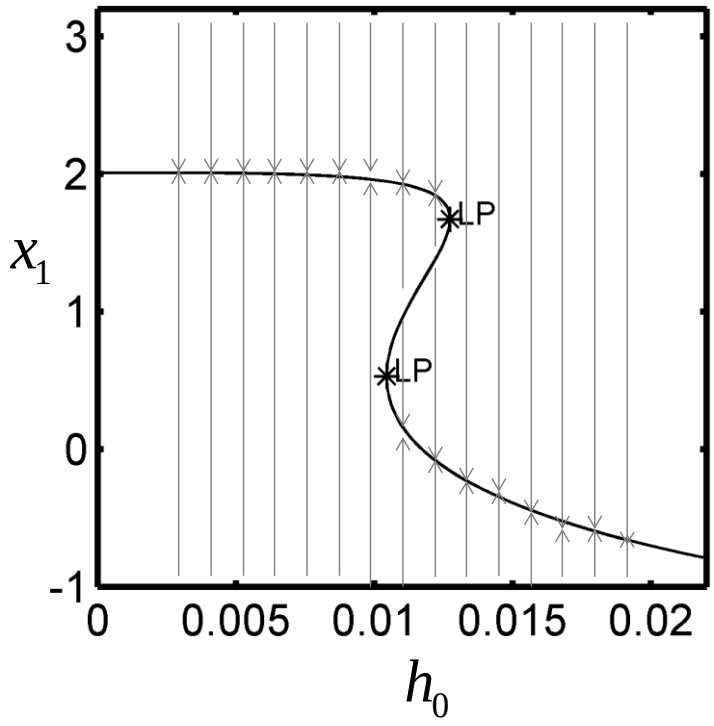

Figure 3.2: Changes in the heterotroph's relative body size along the handling time gradient x_1 and h_0 indicate the heterotroph's relative body size and handling time scalar, respectively, while the stars labelled LP indicate the limit points along the curve. Simulations started with parameter values: k_0 = 0.01, d_0 = 0.1, μ = 3, M_γ = 10, σ_γ = 1.5, λ = 0.3, q = 0.25, M_K = 1, σ_K = 0.6, r = 10, s_0 = 1.

By carrying out a bifurcation analysis of the model, two limit point bifurcations with respect to h_0 between which there were unstable equilibrium states, were detected, as indicated in Fig 3.2. I also observed a range of values of h_0 for which the system exhibited alternative steady states (bi-stability). This behaviour was consistent even for different levels of cannibalism (depicted by parameter β in equation 3.2.1) in the model (Fig 3.3).

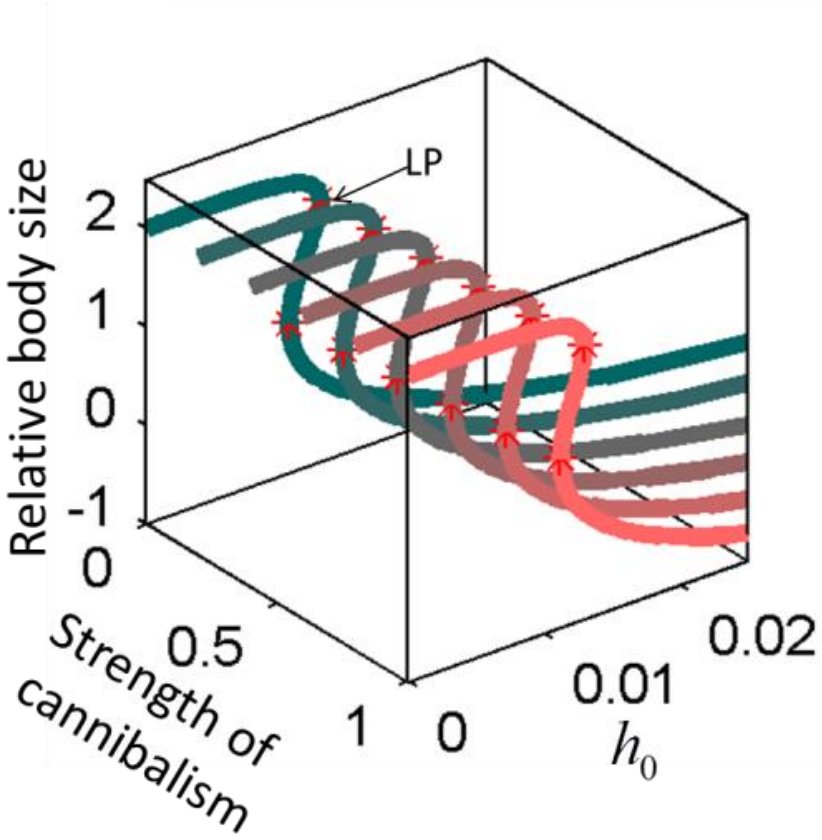

Figure 3.3: Changes in the heterotroph's relative body size along the handling time gradient for different levels of cannibalism. x_1 and h_0 indicate the predator's relative body size and handling time scalar, respectively, while the stars labelled LP indicate the limit point bifurcation. Simulations started with parameter values: $k_0 = 0.01$, $d_0 = 0.1$, $\mu = 3$, $M_\gamma = 10$, $\sigma_\gamma = 1.5$, $\lambda = 0.3$, $q = 0.25$, $M_K = 1$, $\sigma_K = 0.6$, $r = 10$, $s_0 = 1$.

Although the bifurcation analysis, in general, showed that the analytical behaviour of the model with and without cannibalism is the same (compare Fig 2.3 and 3.4), cannibalism seems to enhance the existence of regime shifts. Figure 3.4d, for example, shows that when the bifurcation analysis with respect to the rate of reproduction (r) is carried out with in a system with a cannibalistic predator, tipping points are detected, yet without cannibalism, these tipping points do not arise (compare Figure 2.3d of Chapter 2 to 3.4d).

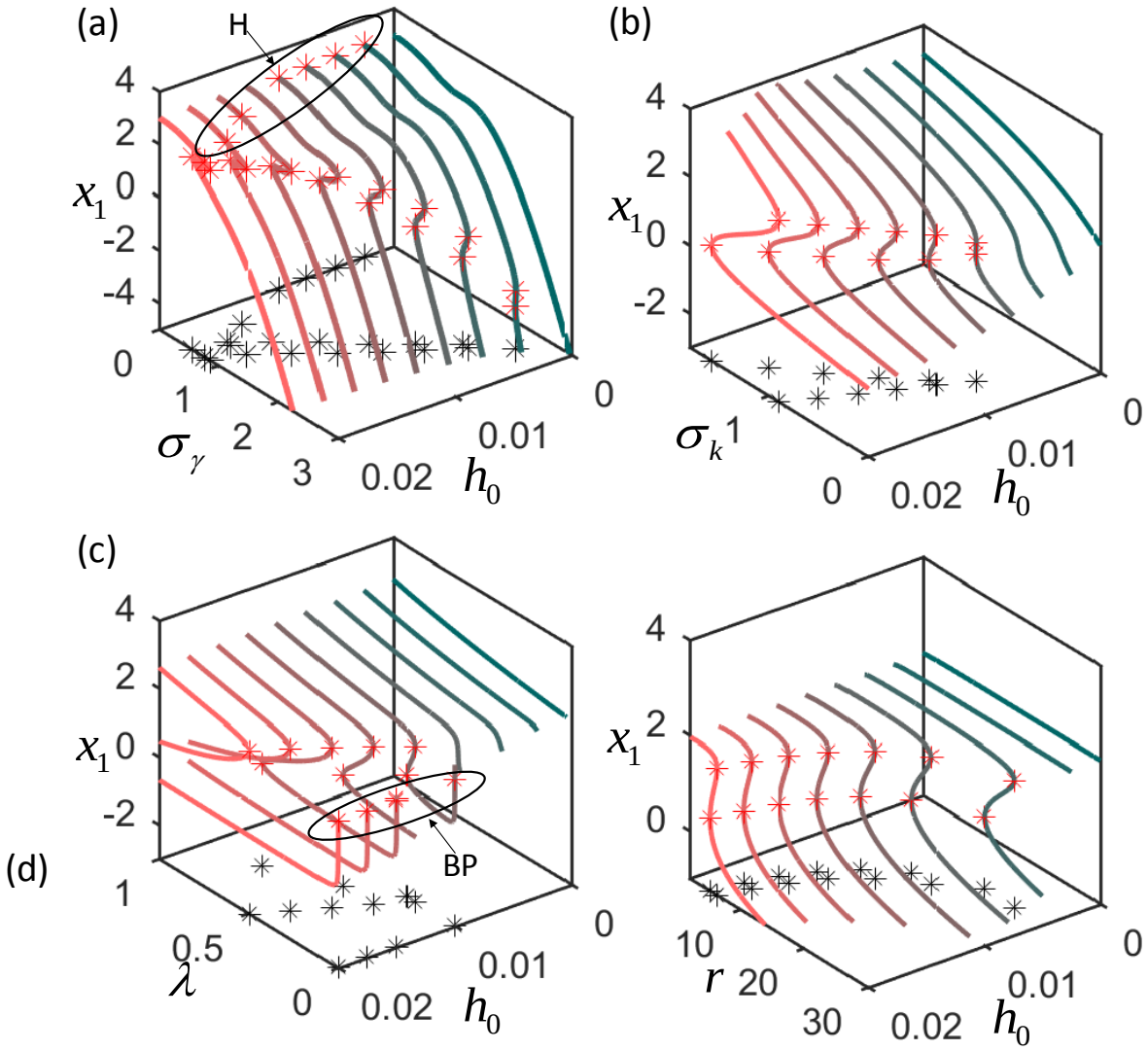

Figure 3.4 Changes in the heterotroph's relative body size with respect to two parameters. For different values of the handling time scalar (h_0), panels (a), (b), (c), and (d) show continuation curves with respect to the standard deviation of the consumption kernel (σ_γ), standard deviation of the competition kernel (σ_k), heterotroph's conversion efficiency (λ) and autotroph intrinsic birth rate (r) gradients, respectively. Each continuation curve corresponds to a different value of the handling time scalar where red indicates the highest handling time. The rest of the parameters are as in figure 1. LP indicating a limit point while H indicates hopf, while BP indicated branching (different from evolutionary branching) bifurcation points.

Cusp points (points at which two limit points meet) during continuations with respect to σ_γ, σ_k, λ and r_g (see table 1 for the summary of the cusp points) were also detected. By comparing Fig 3.4 and Fig 3.5, the cusp point with respect to σ_γ was detected at low values of h_0 and high values of σ_γ (Table 1, Fig 3.5). In addition to the cusp point, a zero-hopf point (where a limit point and hopf point meet) was detected. For σ_k and λ, the cusp point was detected at low values of both the respective parameter and h_0 (Table 1, Fig 3.5).

Table 1: Values of the cusp and zero-hopf bifurcation points in Fig 3.5. C and ZH correspond to cusp and zero-hopf, respectively

Parameter	n_0	n_1	x_1	Parameter value	h_0
σ_γ: ZH C	1.898803 439.361799	0.623245 179.685671	2.983303 -3.722404	0.116820 2.662602	0.162149 0.001967
r	7.604521	0.273380	1.103377	0.176784	0.546961
λ	447.109375	11.895764	1.233854	0.152887	0.007706
σ_k	363.279603	15.182419	0.884158	0.352805	0.007046

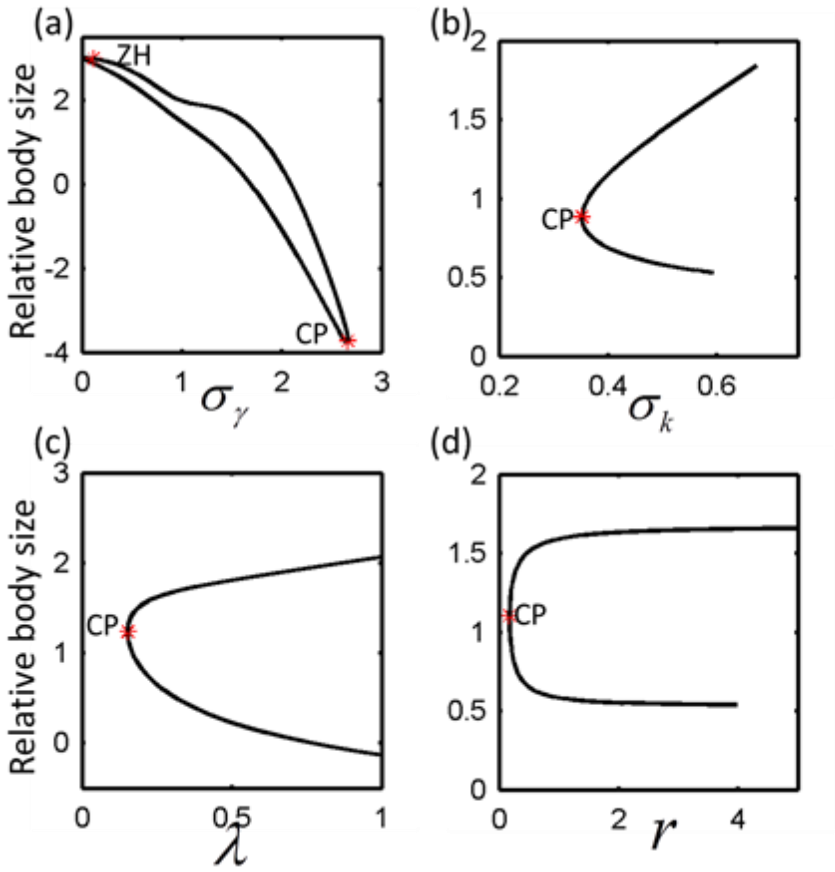

Figure 3.5 Cusp points detected by continuing the limit points in Fig 3.4

To examine how non-linear functional response influences biodiversity, I investigated the possibility of branching events (points of polymorphism) by quantifying the strength of disruptive selection as the curvature of the selection gradient. Figure 5 shows that initially, the strength of disruptive selection increased with h_0 until a certain threshold (corresponding to the limit point, LP, in figure 2) after which it suddenly went high and then started to decrease. I also noted that the strength of disruptive selection was mainly influenced by the competition term in my model as in Chapter 2. In fact, predation terms served to stabilise the system against disruptive selection pressures. However, the stabilising effect of predation gain decreased before the limit point and increased afterwards as handling time increased.

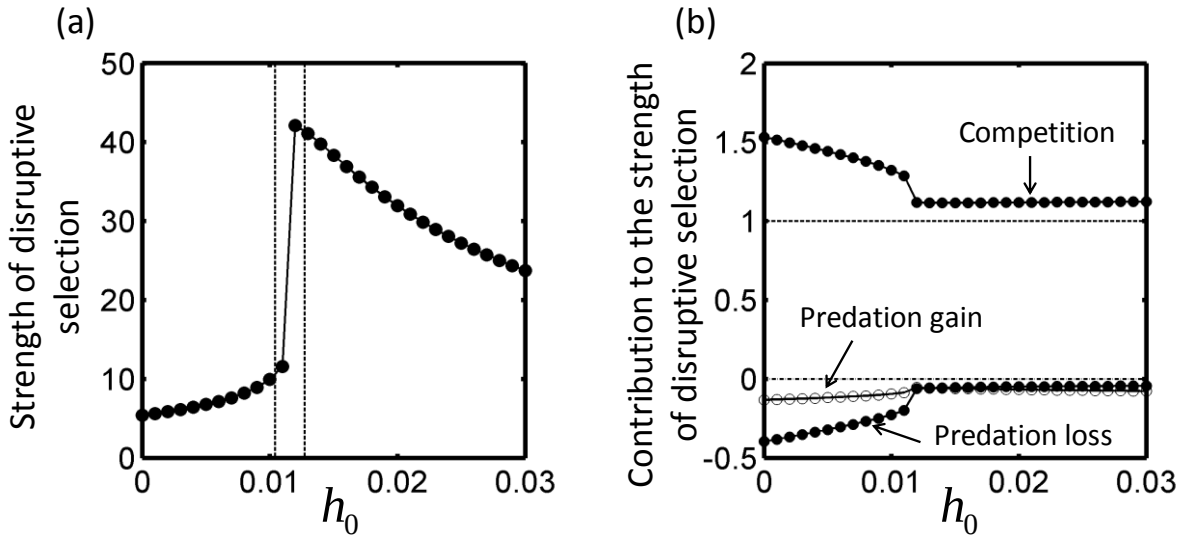

Figure 3.6: Variation in the strength of disruptive selection with handling time. Panel (a) shows how handling time affects the strength of disruptive selection while panel (b) shows the relative contribution of competition, predation gain and predation loss (due to cannibalism in this case) to the strength of disruptive selection. The region between the vertical dotted lines corresponds to the bi-stability region (between the two limit points) in Fig 3.2.

3.3.2 Food web emergence and structure

By tracking the number of morphs when evolution came to a halt, results showed that an increase in the handling time increased the number of morphs in the emergent food-web (Figs 3.7 and 3.8). This increase in the number of morphs was consistent even in the regions of bi-stability and regime shifts. I also noted that an increase in handling time widened the ecological niche of species by introducing smaller and larger morphs in the emergent food web.

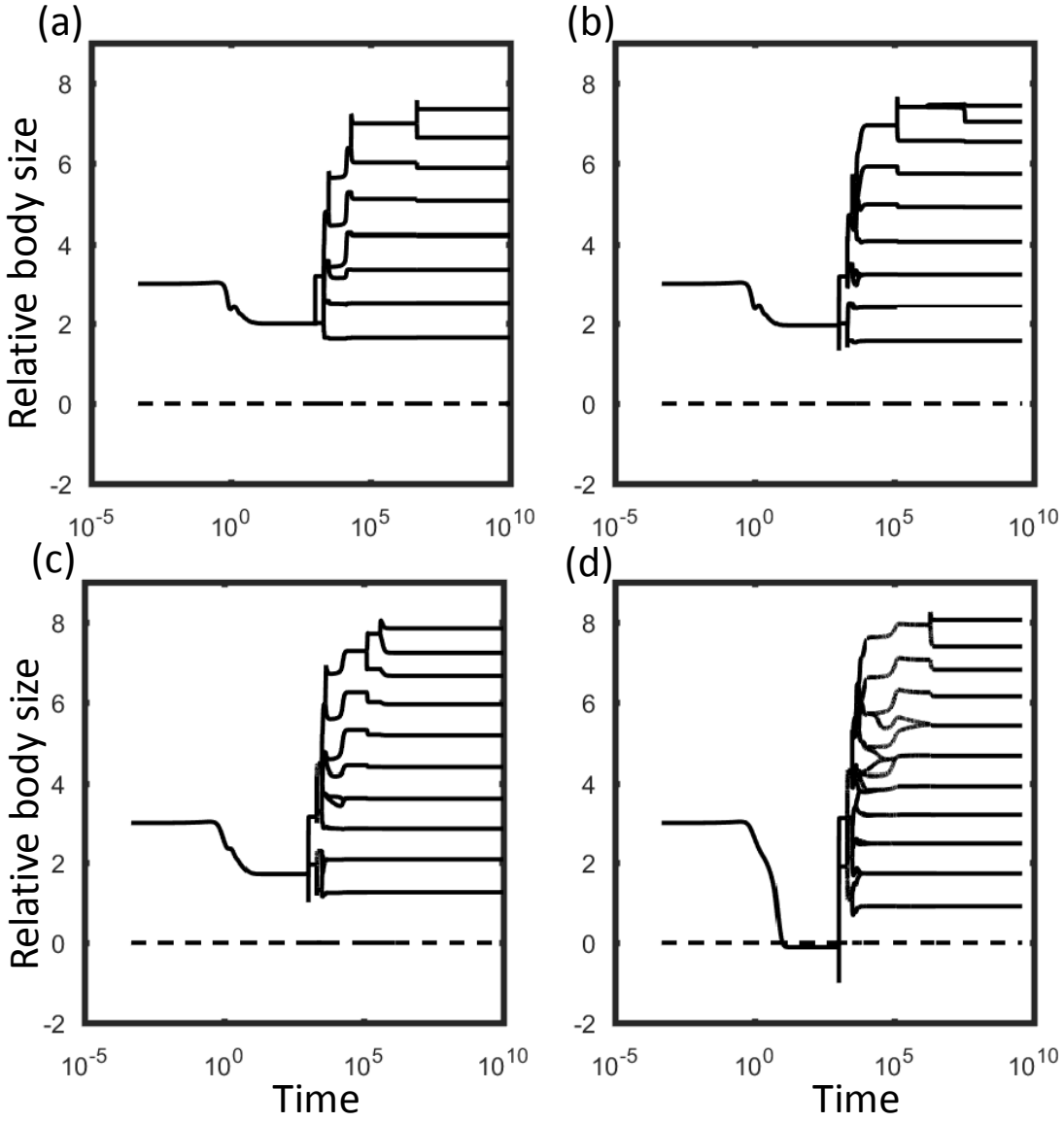

Figure 3.7 Evolved model food-webs under different predator saturation levels (depicted by different handing times). Starting with one autotroph and one heterotroph with the same density (1) and different relative trait values (0 and 3 respectively), panels, (a), (b), (c), and (d) show how 8, 9, 10 and 11 heterotrophic morphs emerge from one when h_0=0.0, 0.005, 0.01 and 0.015, respectively. The other parameter values: k_0 = 0.01, d_0 = 0.1, μ = 3, M_γ = 10, σ_γ = 1.5, λ = 0.3, q = 0.25, M_K = 1, σ_K = 0.6,r_g = 10,s_0 = 1 are the same for each case. The red line is the relative trait value of the autotrophic morph while the blue ones represent trait values for heterotrophic morphs.

Although an increase in handling time increased the total number of morphs, it reduced the average relative body size in the emergent food-web in cases when the emergent number of morphs was the same (Fig. 3.8(a)). However, regardless of the number of morphs, an increase in h_0 resulted in an increase in the total biomass (Fig. 3.8(b)).

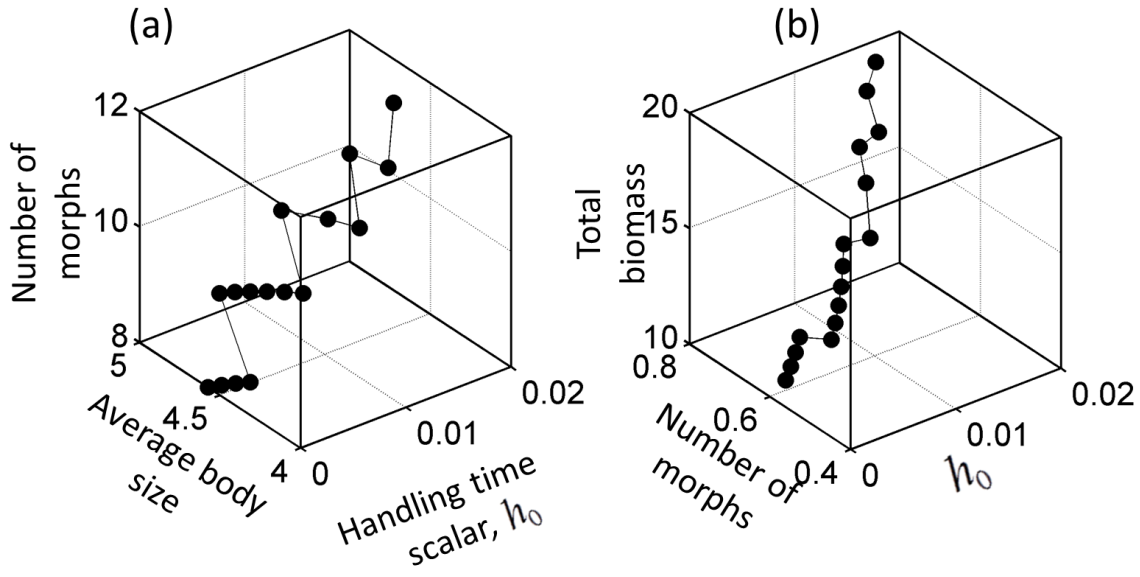

Figure 3.8 The relationship between handling time and number of morphs and total biomass. Panels (a) and (b) show the relationship between h_0 (the constant of proportionality in the equation that describes handling time) and the number of morphs in the emergent food-web and the total biomass, respectively. The colour codes in the two panels indicate the average trait value and average density of the emergent food-web, respectively.

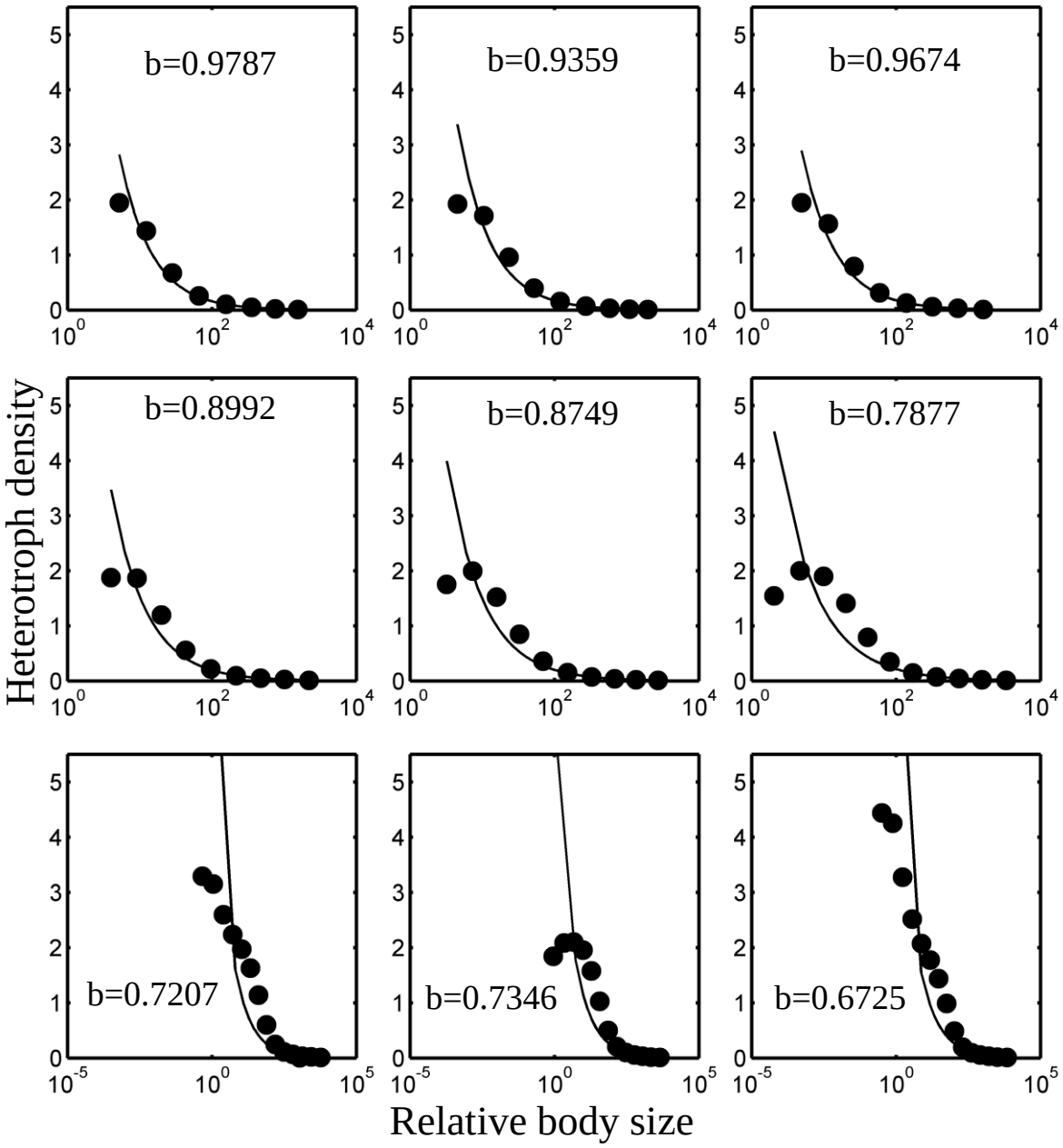

Figure 3.9 Density-body size ratio relationship. Panels represent the density-body size ratio relationship for different emergent food webs. The body size ratios are all relative to the size of the autotroph body size. All simulations started from the same initial conditions with the same parameters, except for the h00 (the constant of proportionality in the equation that describes handling time). Other parameters are k_0 = 0.01, d_0 = 0.1, μ = 3, M_γ = 10, σ_γ = 1.5, λ = 0.3, q = 0.25, M_K = 1, σ_K = 0.6, r_g = 10, s_0 = 1. The value of 'b' in the panels indicates the exponent of the power law fitted solid line.

While testing the EER, I noted that for low handling times, the relationship between the density and body size fairly fit the power law distribution while for higher handling times, it deviated from the power law (Fig 3.9). In fact, for higher handling times, a hump-shaped density-body size relationship emerged implying that the maximum density was attained at intermediate body size. Interestingly, when I fit the power law, the exponents were in the observed range, according to Brown and West (2000), although the intercepts were far from reality.

3.4 Discussion

Using a co-evolutionary model, under the umbrella of adaptive dynamics, I showed how food webs emerge from a single ancestor whether predators exhibit cannibalism or not. In fact, since cannibalism does not affect the analytical behaviour of my model, I will hence forth discuss results from the food web model only, without necessarily ignoring its rare potential to enhance regime shifts. The Adaptive dynamics approach has been previously used to understand how body size relates to many characteristics and properties (Loeuille and Loreau 2006; Brannstom et al. 2011) of organisms and their populations (Peters 1983). The EER, which predicts that the amount of energy used by the various species, should be independent of body size, is one of those that have been debated the most. Some of these debates have arisen as a result of the difference in assumptions made in theoretical studies or the data used in empirical ones. As a result, some studies have confirmed while others refuted the EER saying that the relationship between density and body size is hump-shaped as opposed to the power law. In fact, Loeuille and Loreau argued that the EER is nothing but a hypothesis. In what follows, I discuss why this could be true following my study.

First, I consider how body size influences functions such as the handling time, $h_{ij} = h_0 s_j s_i^{-0.75}$ as this is a reality that some previous theoretical studies have ignored. In 2010, Vucic-Pestic et al. conducted an experiment in which they showed that 89% of handling time was explained by predator and prey body mass. Handling time consists of three main processes: search, capture and digestion time. If we assume that the gut and the stomach size are proportional to the body size, then the maximum ingestion will also be proportional to body size.

Consequently, handling time should have an inverse relationship with body size (Vucic-Pestic et al 2010). However, small predators may have a small search area and hence difficulties in subduing prey larger than themselves, thus leading to inefficient attacks while larger predators may have difficulties in catching small prey individuals since small ones have quicker reaction times and higher escape efficiencies. As a result, the capture success decreases with predator-prey body mass ratio above an optimum mass ratio but increases below that which is optimum. With these complex dynamics in mind, the handling time function I considered depends on relative rather than absolute body sizes. This consideration gives my model an advantage over subsequent models which have assumed a constant handling time.

Slight differences in the handling time, like with other functional response parameters, can have drastic consequences for population dynamics, food web structure and stability in natural ecosystems (William and Martinez 2004; Williams 2006; Rall et al. 2008). Using the same model, in Chapter 2, I showed that changes in handling time scalar gives raise to limit point and hopf point bifurcations, which can potentially be interpreted as regime shifts in a system. Interestingly, theoretical studies which have confirmed the EER have assumed the type I functional response during their simulations. My results confirm the power law relationship between density and body size for the type I functional response (handling time = 0) but deviate from it as handling time parameter value increases (Fig 3.9). The smaller morphs which get

introduced into the system as the handling time increases may have low densities due to having most resources larger than they are. This could influence their density, hence the hump shaped relationship.

Previous studies have also shown that the EER emerges only if species have a common resource or at least the same amount of resources (Carbone and Gittleman 2002; Brown and Gilloly 2003). However, we intuitively know that body size determines who consumes whom. Mostly, small species may hardly consumer large ones, a constraint I explicitly considered in the model through the function γ_{ij}. In addition, some species turn out to be specialists while others become generalists during the process of co-evolution. It is therefore not possible for all species to have the same resources or even an equal amount of resource. Loeuille and Loreau (2006) argue that for larger niche width, the EER is strongly supported and obviously, in a community with large niche width, every species may have access to all possible resources; however, foraging theory stipulates that species concentrate their energies on a selected number of resources rather than all the available resource (Stephens and Krebs 1986). This principle has predicted organisation structures that are 90% similar to observed ones (Nuwagaba et al, 2015). I therefore strongly believe that even in cases of large niche width, the fact that species still select a subset of available resources as their own cannot make us arrive at the EER.

Damuth (1981) speculated that EER may emerge from co-evolving interacting species; however, I allow food webs to emerge from co-evolution with body size as the evolving trait and still do not support the EER. Many studies have suggested that body-size difference between consumers and preys may have important implications for population dynamics, hence food web structure, function and evolution (Brose et al 2006). For instance, some invertebrates have optimised their morphology and physiology to allow effective handling of large bodied preys. Spiders, for example, use toxins and external digestion to consume prey of an equal size

as themselves while other invertebrates are suctorial, which allows them to handle larger prey. This puts such species in a higher trophic level, less density even though small in body size.

In Chapter 2, I observed instances where predators had prey that were larger than they were at the first evolutionary singularity. In such cases, one may be quick to assume that such a scenario is an outlier in a bid to support the EER. This hump-shaped relationship between body size and density in my model emerges from co-evolving species' interactions, and it would not be wise to treat any cases as outliers.

It was interesting to note that although the EER is not supported by my adaptive co-evolutionary model with type II functional response, the biomass production in the system increased with handling time. Total biomass and hence productivity increases with handling time and biodiversity. This could imply that whether the EER holds or not, other relationships within the food web may still not be affected. Speculations have indicated that lack of a direct measurement of energy flux makes it difficult to confirm the EER. However, Loeuille and Loreau (2006) computed the energy flux and still contradicted the theory. In my model, the computation of energy flux would consider the species' handling time, which depends on species body size. Consequently, energy flux would not be independent of body size. Although I may not consider it a meaningless uninformative concept as stipulated in Isaac et al. (2013), I agree that the EER does not hold in most cases. Whether Damuth's theory holds within a guild or the same trophic level remains to be investigated.

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CHAPTER 4

How important are propagule pressure, body size and handling time for invasion success?

"Throughout history, men have tried to play God by moving rabbits, goats, sparrows, mongooses, and a hundred other species to oceanic islands and island continents, and later have wished to God they hadn't."

Victor B. Scheffer, in The Year of the Seal

ABSTRACT

Biological invasions are currently one of the greatest threats to biodiversity. However, evolutionary changes have made it almost impossible to predict their next move. Unfortunately, not much is known about the factors that enhance invasion success in the face of evolution. I used a mathematical model of co-evolution to investigate both the propagule pressure and diversity-invasibility hypotheses in co-evolving food webs. I found no support for the former but support for the latter. The former is only true when there are empty niches in the food web. In addition, I investigated the role of handling time and body size difference between the potential invader and the average native individuals and found that larger invaders in a conducive environment thrive better than their smaller counterparts which are often outcompeted by the natives. Increasing handling time, which reduces feeding efficiency, increases chances of invasion success (see this in results and discussion) due its creation of empty niches. Generally, the availability of niches was the most outstanding factor for invasion success.

Keywords: Invasion, propagule pressure, biodiversity, handling time, body size, niche.

4.1 Introduction

Humans have moved from place to place often carrying along with them different species, sometimes intentionally and sometimes not. Some of these species which have been moved from regions in which they are native to areas in which they do not naturally occur have caused significant changes to recipient ecosystems (Lovett et al. 2016; Blackburn 2014). Although most of these changes have been considered negative, others have been positive. For example, in their study of marine invaders, Katsanevakis et al. (2014) found that although 65% of them had a negative impact on other species, 35% of them had a positive one. Consequently, some

authors have argued that we should rather be concerned about which species affect the ecosystem and how they do so, rather than which species are alien or native.

Invaders are usually identified by their resource exploitation (Alexander 2014). Moreover, Catford et al (2009) noted that 28 out of 29 invasion hypotheses which existed then depended on the difference in resource use. In an experiment on Cray fish from Bolton Abbey and Wyke Beck, the invasive crayfish (*P. leniusculus*) did not only consume 83% more prey overall than did its native competitor (*A. pallipes*) when offered a range of food items but also preyed at a 10% higher rate and showed less 'choosiness'. In a meta-analysis of field experiments with mammalian and avian predators, Salo et al. (2007) revealed that the impact of alien predators was double that of the native ones. Subsequently, there has been a movement into understanding the functional response (relationship between resource availability and resource consumption rate (Solomon 1949; Holling 1959a, b; Juliano 2001) of aliens and how this strategically positions them in a new environment. It is most likely that comparing functional responses of known invaders or perhaps new ones and their comparable natives could allow more reliable predictions of the impact of invaders in communities.

Most of the functional response based studies have been done in the lab or during field experiments. These experiments are good and informative; however, it is very important that current research goes past the describing and recording of case studies into the development of a mechanistic understanding of the impact of invaders (Walther et al. 2009; Dick et al. 2013; Simberloff et al. 2013). This is where mathematical tools come in handy. Using the theory of adaptive dynamics, studies have shown that food webs can emerge from a single ancestor (Brannstrome et al. 2011; Louarel and Lorel 2006, see Chapter 3). These emergent food webs have been studied to identify factors that influence disruptive selection in an evolutionary process. Following this, it is important to understand how potential invaders, which are

introduced in such an evolving food web, alter the system. This could shade light onto some mechanisms, species traits and properties that enable or inhibit invasion success.

Other common predictors of invasion success have been propagule pressure (Lockwood et al., 2005) and species' traits. In particular, propagule pressure has been used to understand how (1) the propagule size (the average number of individuals involved in a single release event) and (2) the propagule frequency (the average number of release events per unit time) influence the invasion success of the introduced species (Lockwood et al. 2005, 2009; Blackburn et al. 2009; Simberloff, 2009). On the other hand, trait comparisons have been used to investigate possible correlations between species body size, brain size, body length, etc. and invasion success. In general, propagule pressure correlates positively with establishment and level of invasion while the comparison between the invader and the native traits has shown inconsistent success especially among animal taxa (Hayes and Barry 2008). In fact, although Gonzalez-Suarez et al. (2015) stated that intraspecific morphological traits are strong predictors of invasion success; other studies have revealed that mean trait values are relatively unimportant (Jeschke and Strayer 2006). I argue that it may be important to mechanistically understand how the propagule pressure and body size together contribute to the invasion success of introduced species.

The diversity-invasibility hypothesis, which was previously known as the biotic resistance hypothesis, assumes that in communities with many species, potential invaders may fail to establish due to competition and antagonism from other resident species (MacNeil et al. 2013; Levine et al. 2004). This could imply that when species are introduced in a co-evolving system in which many niches are not filled, the invader may easily invade as compared to one in which most niches are occupied. Overall, the diversity-invasibility hypothesis has received equivocal support (Maron and Marler 2007; Havel et al. 2005a, 2005b; Dunstan and Johnson 2004). I

argue that the differences could have been due to introductions made at different stages in the co-evolution process of the systems in which the introductions were made.

In this study, I used the co-evolutionary model in Chapter 3 to investigate the influence of (i) the initial propagule pressure, (ii) the time of new species introductions in an evolutionary cycle (iii) the difference in body-size between the potential invading species and native species and (iv) the predator's handling time on the invasion success of the new species.

4.2 Methods

4.2.1 The model

The model in section 3.2.2 of Chapter 3 was used here to investigate the influence of an invader on a community of coevolving native individuals. Therefore, consider a basal autotrophic resource ($i = 0$) and p heterotrophic morphs with population densities ($n_i; i = 1,2,..., p$) such that each morph is associated with a value s_i (interpreted as its average mass). While defining the trait value (relative body size) of each morph as $x_i = \ln(s_i / s_0)$, the dynamics of the heterotrophic and the autotrophic morphs can be described by following equations:

$$\dot{n}_i = -d(x_i)n_i + \sum_{j=0}^{p} \lambda \frac{s_j}{s_i} F_{ij}(\vec{n}, \vec{x})n_i - \sum_{j=1}^{p} F_{ji}(\vec{n}, \vec{x})n_j - \sum_{j=1}^{p} M_\alpha \alpha_{ij} n_i n_j, \qquad (4.2.1)$$

$$\dot{n}_0 = rn_0 - \sum_{j=1}^{p} F_{j0}(\vec{n}, \vec{x})n_j - k_0 n_0^2$$

where all parameters and evolutionary dynamics are defined as in section 3.2.2.

For each co-evolving food web, a potential invader was introduced, and four different cases were considered.

1. ***The body size of the potential invader relative to the average body size of the resident individuals***

Three different relative body sizes were considered i.e. 3/4, 1, 5/4 of the average relative body size of native individuals. This was to investigate whether the difference in body size between the native and invader impacts on the invasion success and total biomass of the emergent food web. I considered the three value cases to cater for scenarios (i) when the potential invader is smaller than the average body size of the native individuals, (ii) when the potential invader has the same size as that of the average body size of the natives and (iii) when the potential invader has a bigger body size compared to the average body size of the natives.

2. ***The initial propagule pressure/ density of the potential invader***

I considered four values for the initial propagule pressure / density i.e. $e^{-9}, e^{-7}, e^{-5}, e^{-3}$ to investigate whether the initial density of the invader influences its invasion success.

3. ***The time during the co-evolution process at which the invader is introduced into the co-evolving system***

I considered two different times of invasion during the co-evolution process of food web development (i) before any polymorphism occurs in the system and (ii) after polymorphism. I considered t=400 because at this point, the ecological dynamics are already at equilibrium although still far from the point at which I would allow polymorphism to occur. This was to give the system time to reorganise after the introduction of the potential invader. The second time was t=6000. At this time, polymorphism has occurred a number of times that the diversity in the system has increased. In this case, I am testing the complexity-stability hypothesis, where stability is measured as resistance to invasion and complexity as biodiversity.

4. ***The handling time scalar of the predators in the system of coevolving individuals***

As previously done in Chapters 2 and 3, I also investigated the influence of nonlinear functional response in the evolutionary dynamics of the invasion. I considered three values of the handing time scalar one from each region (before the limit point, between the two limit points and after the limit points) in Fig 3.2 in Chapter 3 to understand how the presence of bi-stability may influence invasion success.

4.2.2 Numerical simulations

For each case, I run the simulation starting with initial conditions as in Chapter 3. The simulations were run until an ESS was reached in most cases, otherwise the simulation was terminated after 10^{50} time steps. Although termination was induced in some cases, all simulation reached a pseudo-equilibrium state at an evolutionary scale. I tracked the changes in body size and density of individuals with time. I also tracked the evolutionary history of the individuals to determine which individuals went extinct and whether they evolved from the native or invading individual, and in each case, I quantified the total biomass in the emergent food webs.

4.3 Results

Simulations from my co-evolutionary model showed that biodiversity in any emergent food web at an evolutionary steady state (ESS) was not affected by introductions of any potential invaders.

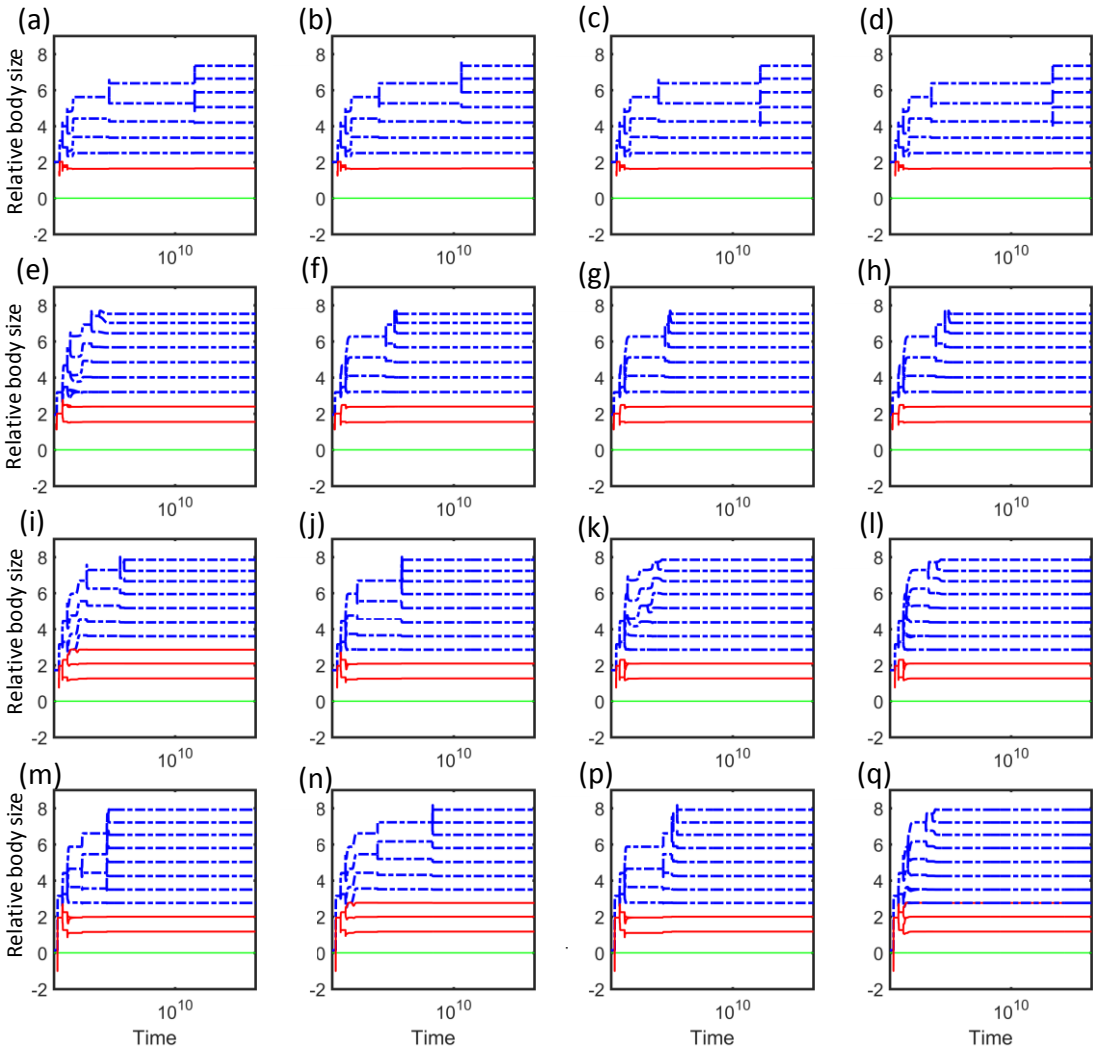

Figure 4.1: The influence of potential invaders of a smaller size than the average body size of native individuals before polymorphism. Introduced individuals were ¾ the average body size of native individuals, and they were introduced at t=400. Panels (a)-(d) correspond to introductions in a system where the handling time scalar was $h_0 = 0$ (linear/type I functional response). Panels (e)-(f), (i)-(l) and (m)-(q) correspond to introductions into systems where $h_0 = 0.005$, $h_0 = 0.011$ and $h_0 = 0.012$ respectively. Panels (a), (e), (i) and (m) correspond to introductions with the potential invader's initial density equal to e^{-9} . (b), (f), (j) and (n) to e^{-7} , (c), (g), (k) and (p) to e^{-5} while (d), (h), (l) and (q) to e^{-3}. In each panel, dotted blue lines correspond to time series of native individuals, solid red lines to introduced individuals and their evolutionary history while the green solid line is the autotroph.

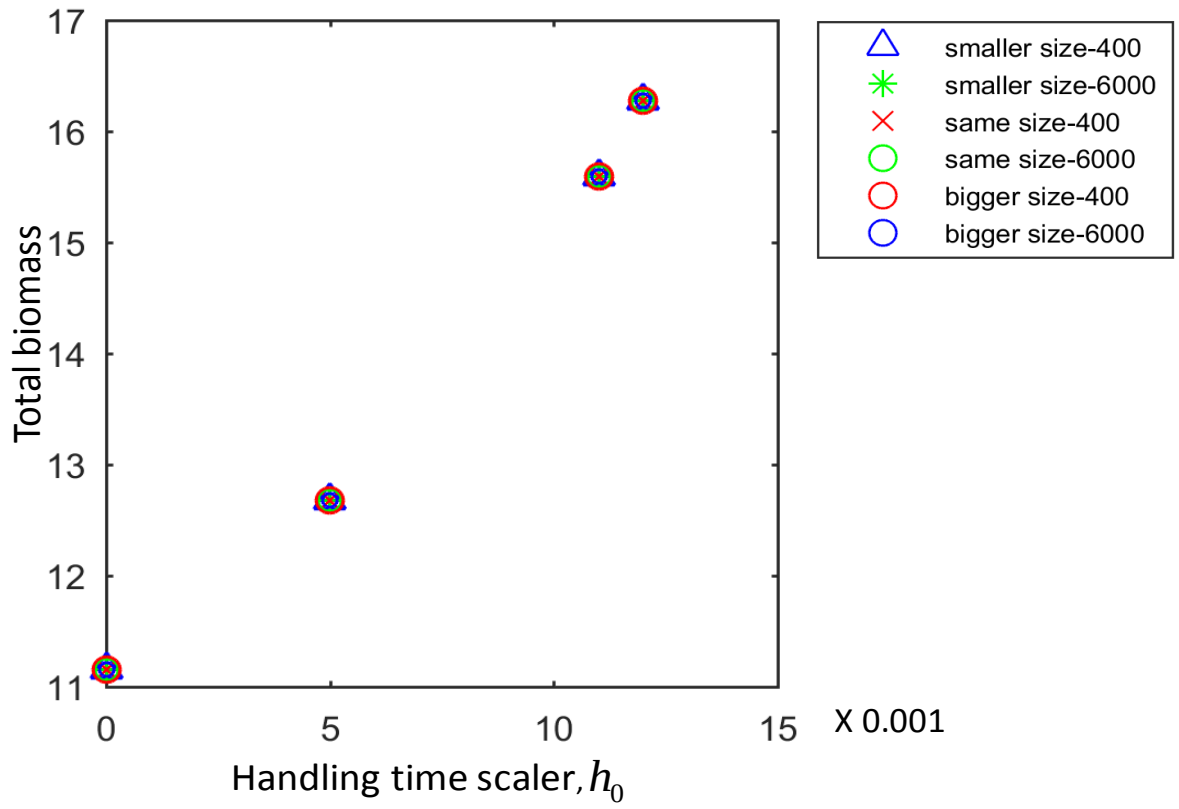

Figure 4.2: Total biomass of invaded food webs relative to different handling time scaler and the time of invader introduction. The data used here corresponds to food webs (a), (e), (i) and (m) in Figs 4.1, 4.3, 4.4, 4.5,4.6 and 4.7.

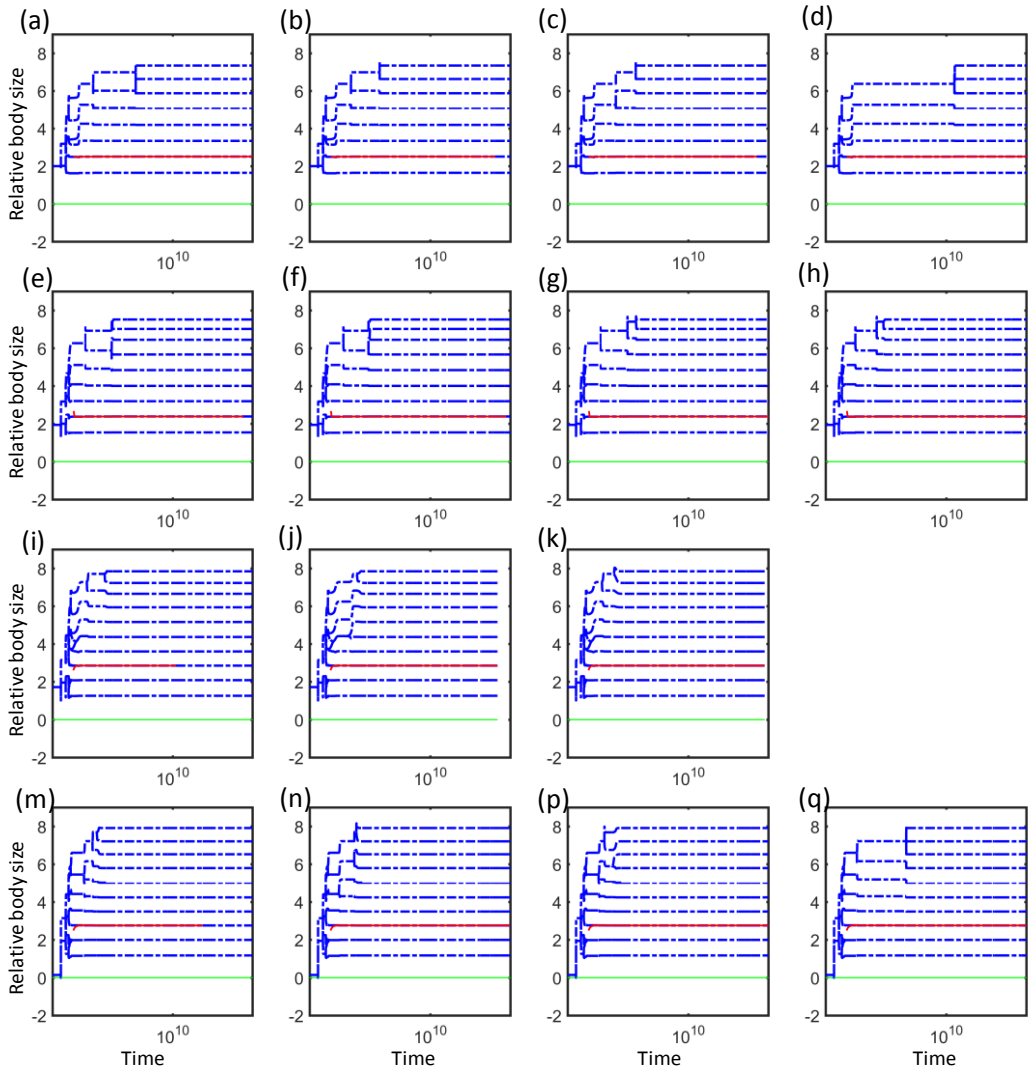

Figure 4.3: The influence of potential invaders of a smaller size than the average body size of native individuals after polymorphism. Introduced individuals were ¾ the average body size of native individuals, and they were introduced at t=6000. Panels (a)-(d) correspond to introductions in a system where the handling time scalar was $h_0 = 0$ (linear/type I functional response). Panels (e)-(f), (i)-(k) and (m)-(q) correspond to introductions into systems where $h_0 = 0.005$, $h_0 = 0.011$ and $h_0 = 0.012$ respectively. Panels (a), (e), (i) and (m) correspond to introductions with the potential invader's initial density equal to e^{-9} . (b), (f), (j) and (n) to e^{-7} , (c), (g), (k) and (p) to e^{-5} while (d), (h) and (q) to e^{-3}. In each panel, dotted blue lines correspond to time series of native individuals, solid red lines to introduced individuals and their evolutionary history while the green solid line is the autotroph.

For each set of parameters, whether successful invasions occurred or not, the total number of emergent individuals at ESS was the same as for the evolved system in the absence of any introductions (compare Fig 3.7 and 4.1, 4.3-4.7). In other words, although the evolutionary histories of the emergent food web were different in some cases, the number of individuals was the same. In fact, both their relative body sizes and the final population densities were the same. We, therefore, observed that in cases where there were no empty niches, invasion or establishment was not possible. Either the introduced potential invaders went extinct along the way or co-existence of the invader and native of the same body size occurred. As a result, the total biomass was unaffected by propagule pressure and body size ratio in the emergent food webs (Fig 4.2). The only difference emerged for different functional response parameter h_0 (Figs 4.1, 4.3-4.7) as already identified in Chapters 2 and 3.

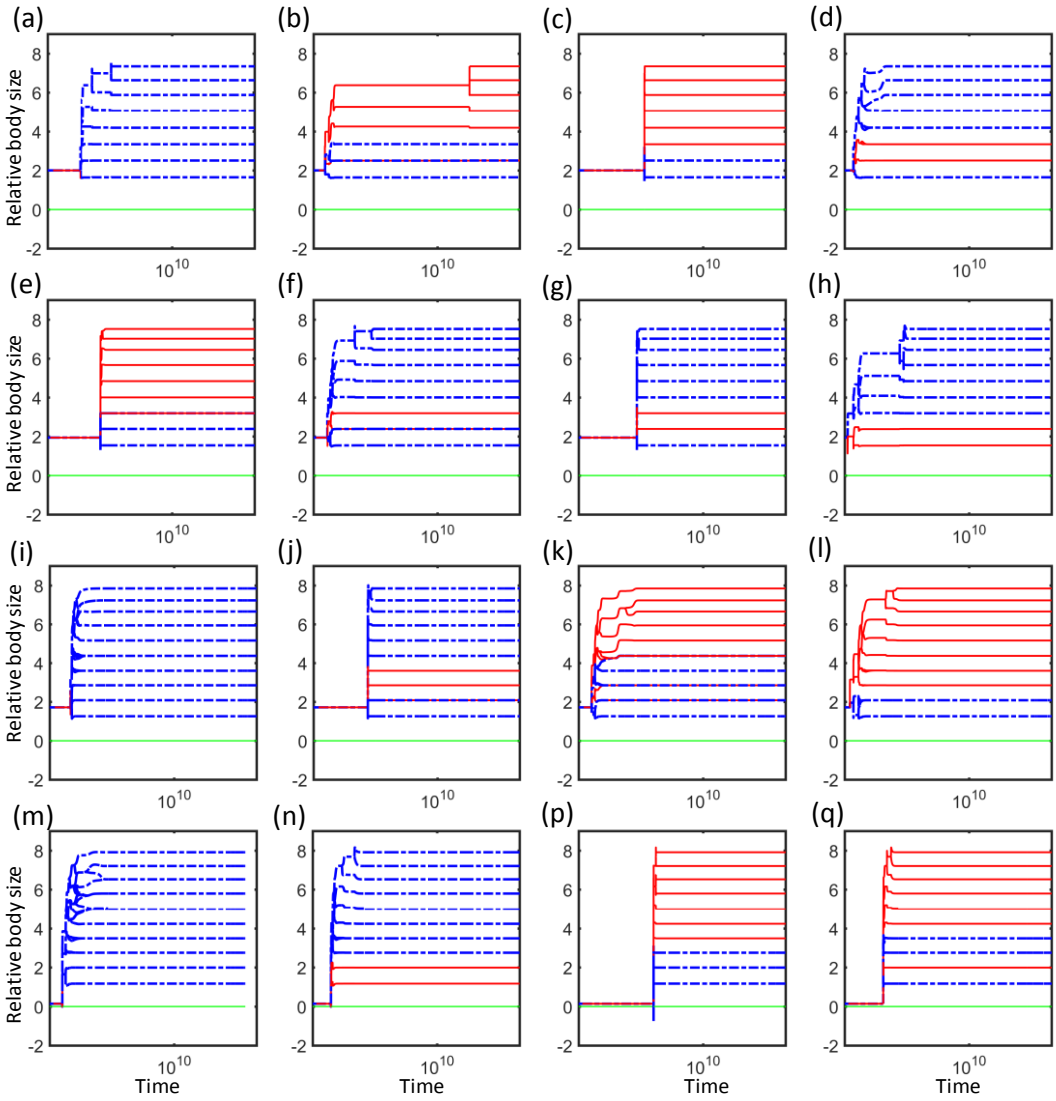

Figure 4.4: The influence of potential invaders of the same size as the average body size of native individuals before polymorphism. Introduced individuals had the average body size of native individuals, and they were introduced at t=400. Panels (a)-(d) correspond to introductions in a system where the handling time scalar was $h_0 = 0$ (linear/type I functional response). Panels (e)-(f), (i)-(l) and (m)-(q) correspond to introductions into systems where $h_0 = 0.005$, $h_0 = 0.011$ and $h_0 = 0.012$ respectively. Panels (a), (e), (i) and (m) correspond to introductions with the potential invader's initial density equal to e^{-9} . (b), (f), (j) and (n) to e^{-7} , (c), (g), (k) and (p) to e^{-5} while (d), (h), (l) and (q) to e^{-3}. In each panel, dotted blue lines correspond to time series of native individuals, solid red lines to introduced individuals and their evolutionary history while the green solid line is the autotroph.

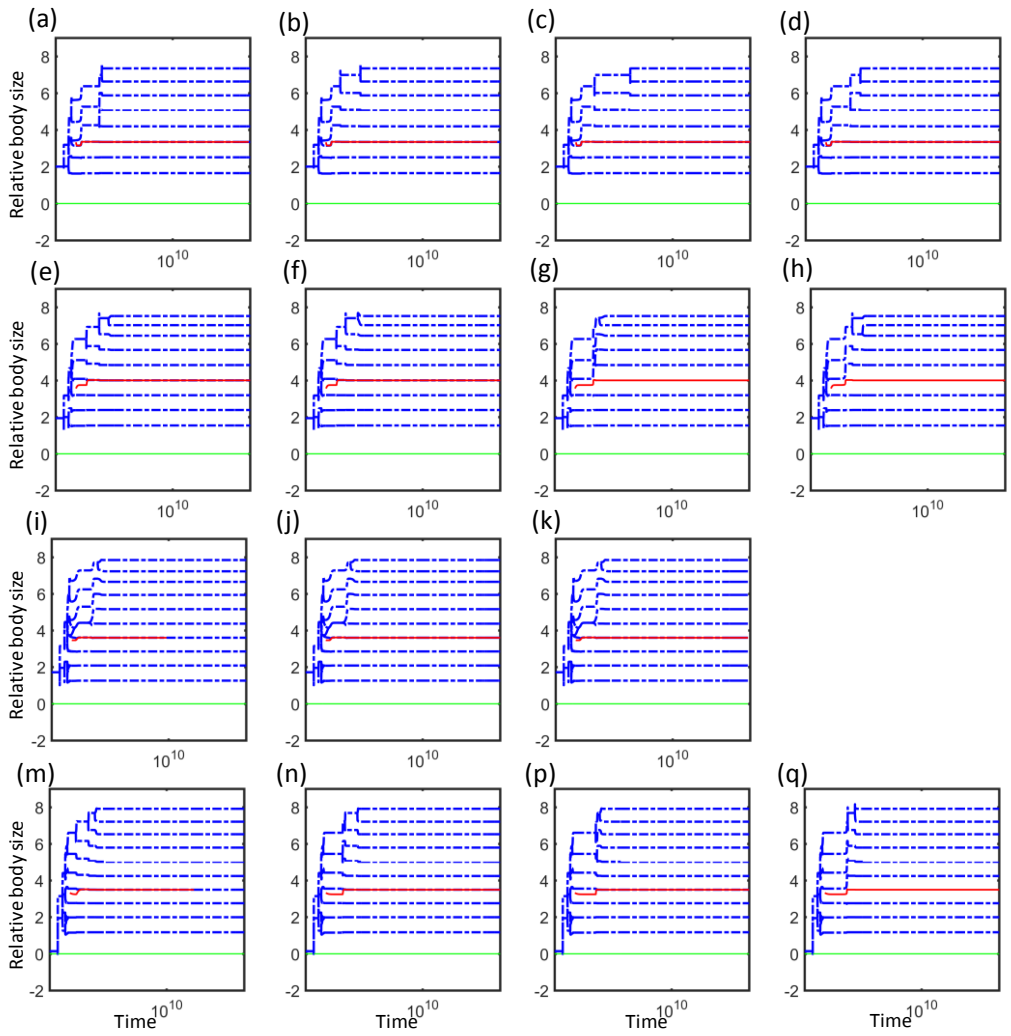

Figure 4.5: The influence of potential invaders of the same size as the average body size of native individuals after polymorphism. Introduced individuals had the average body size of native individuals, and they were introduced at t=6000. Panels (a)-(d) correspond to introductions in a system where the handling time scalar was $h_0 = 0$ (linear/type I functional response). Panels (e)-(f), (i)-(k) and (m)-(q) correspond to introductions into systems where $h_0 = 0.005$, $h_0 = 0.011$ and $h_0 = 0.012$ respectively. Panels (a), (e), (i) and (m) correspond to introductions with the potential invader's initial density equal to e^{-9} . (b), (f), (j) and (n) to e^{-7} , (c), (g), (k) and (p) to e^{-5} while (d), (h) and (q) to e^{-3}. In each panel, dotted blue lines correspond to time series of native individuals, solid red lines to introduced individuals and their evolutionary history while the green solid line is the autotroph.

Although high propagule pressure enhanced invasion success in some cases (figure 4.4 last two rows, 4.6 3rd row, and 4.7 last row) in most cases, its contribution was very unclear. Invasion success was evidently higher when the invader was introduced before polymorphism than when the introductions were made later during the co-evolution process. In fact, although high propagule pressure enhanced the invasion success in some cases, the invasion was very minimal when introduction was made at t=6000. This was consistent even when the handling time was high.

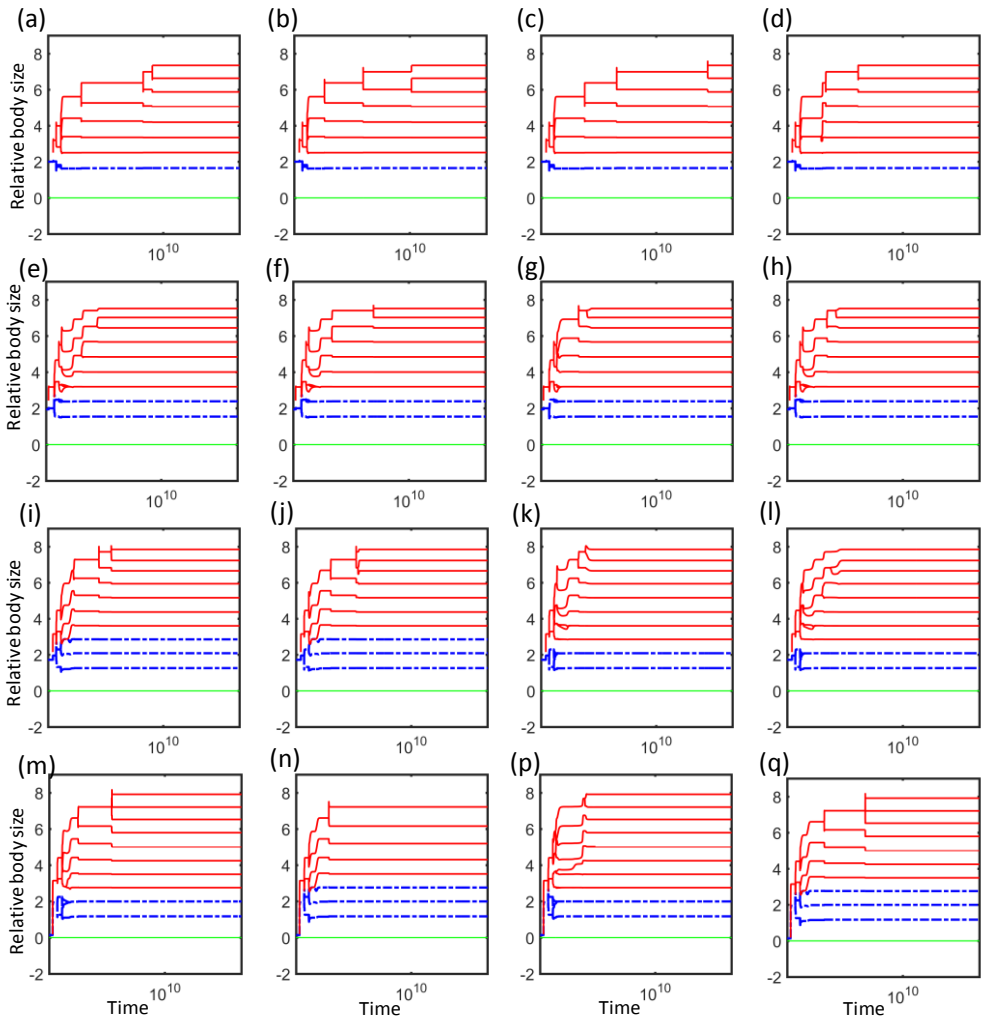

Figure 4.6: The influence of potential invaders of a bigger size than the average body size of native individuals before polymorphism. Introduced individuals were 5/4 the average body size of native individuals and they were introduced at t=400. Panels (a)-(d) correspond to introductions in a system where the handling time scalar was $h_0 = 0$ (linear/type I functional response). Panels (e)-(f), (i)-(l) and (m)-(q) correspond to introductions into systems where $h_0 = 0.005$, $h_0 = 0.011$ and $h_0 = 0.012$ respectively. Panels (a), (e), (i) and (m) correspond to introductions with the potential invader's initial density equal to e^{-9} . (b), (f), (j) and (n) to e^{-7} , (c), (g), (k) and (p) to e^{-5} while (d), (h), (l) and (q) to e^{-3}. In each panel, dotted blue lines correspond to time series of native individuals, solid red lines to introduced individuals and their evolutionary history while the green solid line is the autotroph.

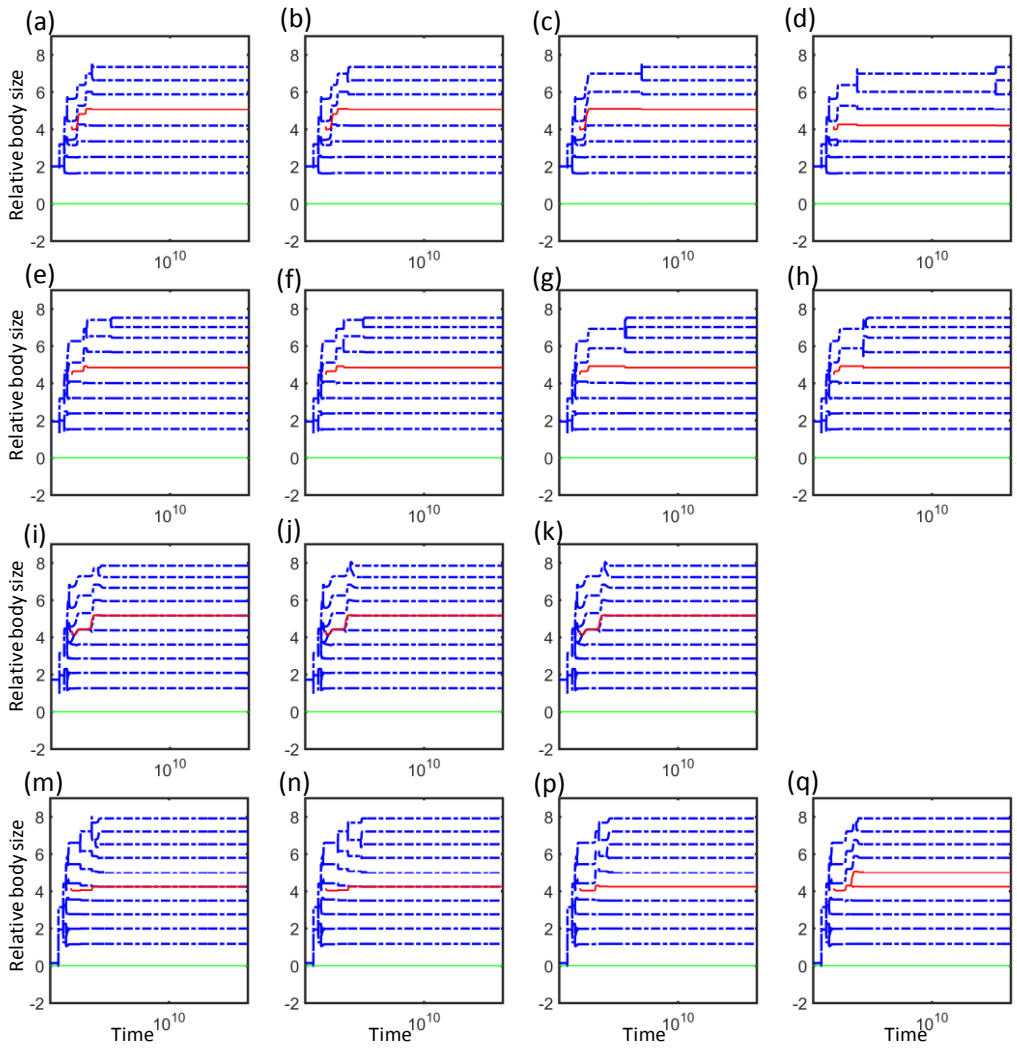

Figure 4.7: The influence of potential invaders of a bigger size than the average body size of native individuals after polymorphism. Introduced individuals were 5/4 the average body size of native individuals and they were introduced at t=6000. Panels (a)-(d) correspond to introductions in a system where the handling time scalar was $h_0 = 0$ (linear/type I functional response). Panels (e)-(f), (i)-(k) and (m)-(q) correspond to introductions into systems where $h_0 = 0.005$, $h_0 = 0.011$ and $h_0 = 0.012$ respectively. Panels (a), (e), (i) and (m) correspond to introductions with the potential invader's initial density equal to e^{-9} . (b), (f), (j) and (n) to e^{-7} , (c), (g), (k) and (p) to e^{-5} while (d), (h) and (q) to e^{-3}. In each panel, dotted blue lines correspond to time series of native individuals, solid red lines to introduced individuals and their evolutionary history while the green solid line is the autotroph.

The influence of body size was evident in some cases and not in others. In cases where the potential invader's relative body size was smaller than that of the native, the possibility of invasion was very low even when the propagule pressure was relatively high. However, whenever the potential invader's relative body size was greater or equal the average body size of the native individuals' one, propagule pressure influenced the invasion success. In general, although the propagule pressure, handling time and body size differences all contribute to the invasion success, my results show that none does it in isolation.

4.4 Discussion

Using data on bird communities on the Hawaiian Island of Oahu, Allen et al. (2015) argue that increasing species' richness and community saturation enhances invasion resistance. They explain that the increase in competition that comes with community saturation advantages the natives which can thrive better than any new species in the given environment. In this study, whenever polymorphism had occurred, it was less possible to have the potential invader successful even when its propagule pressure was high or even when the body size of the invader was higher than that of the average natives. This could indicate that for any food web, specific niches need to be filled, and if an invader is introduced into a community without any empty niches, it may be impossible for it to invade (Figs 4.3, 4.5 and 4.7). I therefore anticipate that whenever invasions have been successful, it is most likely that the potential invader found unoccupied niches present in the area. Moreover, previously in Chapter 2, I observed that an increase in handling time increases the diversity of the emergent food web. The reason why low handling time showed high invasion success could be that the diversity was then low hence the diversity-invasibility hypothesis. In fact, Allen et al. (2015) showed that whenever failed introductions have been recorded, the number of species present in the community is higher.

The most agreed upon hypothesis in invasion biology is the propagule pressure hypothesis; however, its generality has been questioned by a number of data analyses (Moulton et al 2011; Nuñez et al.2011; Allen et al 2013). Under this hypothesis, one expects that when the number of introduced individuals is higher, there is a higher chance that these individuals will establish better in the new environment. To a large extent, my results are in agreement with this; however, in cases such as in Fig 4.3, I observed no effect from an increase in propagule pressure. In other words, even if the propagule pressure is high, if there is no space in the system or no empty niches, the competition against the potential invader will be so high that they will go extinct, sometimes without establishing.

Using the New Zealand birds' data, Moulton et al. (2011) suspected that species were successful not because they were introduced in high numbers, but rather that they were introduced in high numbers because the initial releases were successful. This is an indication that some relationships from data analyses could easily be misinterpreted. In 2013, Moulton et al. went ahead and compared records of passerine introductions with propagule size information across multiple regions (New Zealand, Australia and North America). Their analysis compared randomly selected propagule sizes of unsuccessful introductions with those of successful introductions. Using Monte Carlo repeated sampling, they used assumptions biased toward showing an effect but still found no statistical support for the propagule pressure hypothesis. Although this is often an unexpected result, it forms part of the larger pool of studies that questions the role of propagule pressure in invasion success.

Whether or not the difference in body size determines which individuals establish in and invade a new environment does not seem clear in the literature. There is a common argument that small body sized individuals have a higher chance of establishment and invasiveness because they can reproduce faster and have many offspring in a short time (Allen et al. 2013). On the other hand, some studies show that large body sized animals are able to survive because they

stay longer and could adapt to the new environment easier than their smaller counterparts whose lifespan is short (Capellini et al 2015). I argue that none of the arguments can be generalised because the influence of body size is never in isolation.

Although they emphasised the fact that they just used associations which were not evidenced by lab or experimentally tested causes, Jeschke and Strayer (2006) showed that neither of the body mass, body length, and brain mass was a good predictor of invasion success during their study. In fact, although Allen et al. (2013) had support for a negative relationship between body size and invasibility of individuals, they dropped the idea in 2015, thereby questioning the relevance of body size as a predictor of ecological processes in general and not just in invasion. Using my model, I showed that body size could be used as a predictor only when one is sure that empty niches are present (compare Figs 4.6 and 4.7). Otherwise, its relevance is insignificant.

Nonetheless, the influence of body size can be engineered by human intent. For example, one may be interested in production of specific body sized individuals and do all it takes to have those individuals establish in a new environment. Unfortunately, such biases are not easy to isolate during data analyses. As a result, conclusions from data analyses could skew toward species of specific interest to humans. For example, large highly productive mammals may have a higher chance of establishing or even invading but mainly because humans have an interest in their productivity. In other cases, the small ones are easy to establish because they are easy to transport from place to place (Jeschke and Strayer 2006). In this study, I found that the final body sizes and population densities of the individuals in the emergent food web were not affected by changes in the difference between body size of the potential invader and that of the average natives. As a result, all the food webs that emerged had the same total biomass (sum (density x body size)). If one is interested in how the total biomass of the system is affected, my results suggest that an invader pauses no threat. This points to the fact that the

greatest threat of invasive species may not necessarily be productivity but rather biodiversity loss, rendering productivity or biomass as invalid measures for impact of invasion on a system (Capellini et al 2015).

Although most of the studies that have studied the functional response in invasion biology have been empirical, using a mathematical model, I have shown that a potential invader introduced at any time during the co-evolutionary process most successfully invades if the predator's handling time is high enough. In most cases, investigations have considered the influence of the functional response of the potential invader on the system of native individuals rather than the functional response of the whole system of interacting species. In my model, I monitored the influence of a general increase in predators' handling time (increasing the non-linearity of the functional response) on the invasion success and found that non-linear functional response promotes invasion success.

Intuitively, if resource use is slow, there is always enough food to accommodate more consumers and hence any potential invader introduced into such a system should be able to at least establish. Unfortunately, the mechanisms that influence handling time in ecosystems are not very clear. Temperature is, so far, one of the identified factors that influence a predator's handling time (Wu et al. 2011). A deeper understanding of how temperature affects handling time may be paramount to forecast future invasions. In fact, one wonders why invasions/ invasive species are more common and catastrophic today. Could this have something to do with climate change? Both scientific and non-scientific viewpoints have shouted about the reality around climate change and its implications. Unfortunately, many others have maintained a deaf ear for whatever reason. From this study, I strongly recommend that both theoretical and imperial studies are done together to better understand the implications of the heating planet on the processes such as metabolism and the rest that feed into the handling time, otherwise, invasions will continue to surprise us.

4.5 References

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CHAPTER 5

Conclusion

Not that in nature the relations can ever be as simple as this. Battle within battle must ever be recurring with varying success; and yet in the long-run the forces are so nicely balanced, that the face of nature remains uniform for long periods of time, though assuredly the merest trifle would often give the victory to one organic being over another.

Charles Darwin, in The Origin of species

5.1 Summary

In this thesis, I modelled the eco-evolutionary dynamics, first of a predator and its autotrophic prey. I recognised the fact that the predator's foraging efficiency is dependent on the difference between its body size and that of its prey. By considering the dependence of a predator's handling time (time it takes a predator to process its food item) on the difference between the relative body sizes of both the predator and prey, I showed that an increase in handling time reduces the predator's relative body size in the long run. In fact, reducing handing time in my simulations enhanced the presence of evolutionary regime shifts in predator's body size. These deductions were consistent with respect to coupled changes in handing time and species' niche width, prey's intrinsic growth rate, competition intensity and the predator's efficiency in converting the consumed prey into its biomass. However, I noticed that in the absence of evolution, these regime shifts could be rare. Consequently, investigating the interplay between evolutionary and ecological feedbacks could enhance our understanding of evolutionary regime shifts for better management.

I extended the predator-prey model to provide for polymorphism through rare mutations and directional selection. By allowing the predator and its successive descendants to adaptively evolve, I showed that food webs consisting of predator-prey interacting morphs can emerge. I also tested the influence of non-linear functional response on this co-evolutionary process and found that it increases biodiversity. Both smaller and larger morphs were introduced into the food web whenever the handling time was increased. As a result, food webs generated using higher handling times violated the energetic equivalence rule (the density-body size relationship is power law). The relationship between body size and density for such food webs was hump-shaped, questioning the generality of the commonly known power law relationship.

With the introduction of potential invaders into the system of co-evolving individuals, I tested two of the main invasion hypotheses: (i) the propagule pressure and (ii) the diversity-resistance hypothesis. I found support for the latter and not for the former. Indeed, communities with high diversity are harder to invade than the less diverse ones. Intuitively, an ecosystem can only sustain an optimum number of individuals but not more. On the other hand, propagule pressure was influential only whenever the coevolving food web was still less diverse, indicative of the presence of empty niches. As expected, whenever potential invaders have larger body sizes than the native individuals, their chance of successfully invading increased probably due to their foraging competitive advantage that comes with body size.

5.2 Caveats and future directions

Regardless of how reasonable my model assumptions were, one can always put emphasis on a different aspect of species interactions. For example, allowing the autotrophic prey to evolve could bring light into how the prey defences against predation could influence these co-evolutionary dynamics. Moreover, although my results bring much insight into the role of species functional traits and functional response analysis, its predictive power can only be verified by empirical studies. In the advent of technology, long term data can be collected, accessed and analysed to test some of my claims. For example, instead of clamping all small species in one bin while testing the energetic equivalence rule, previously analysed data could be reanalysed to verify this hump-shaped relationship, especially that I am not the first person to point it out.

I was able to investigate factors responsible for the individual's invasion success in a co-evolving food web. However, food webs today face more challenging anthropogenic

disturbances than just invasion. Habitat loss pauses a greater threat than invasion. Therefore, investigating the impact of other threats would give a wholesome look at the factors that enhance biodiversity loss in co-evolving food webs as a whole. For example, using my approach, one could test co-evolutionary dynamics in the face of species extinctions or habitat destruction in addition to invasion since they all could happen independently.

Some predators have the capacity to remember which prey they encountered before and as a result, decide on their next prey depending on how beneficial their previous encounter was. Including prey switching in my model could point us to understanding how this potential to remember could impact species co-evolution as they struggle to survive in their disturbed habitats.

Appendix: Main code used for analyses in Chapters 3 and 4.

```
%%% The outputs of this functions can be saved in files that could be
%%% accessed for the rest of the analyses.
%%% The strength of disruptive selection is extracted from the function
%%% 'fitness_bis'.
%%% Depending on the various scenarios, new individuals are introduced to
%%% study the invasion cases in chapter 4.

function ESS_state = Evol_food_wed(k0, d0, mu, Mg, sg, l, q, MK, sK, rg, h00)

% Evol_food_web(0.01, 0.1, 3, 10, 1.5, 0.3, 0.25, 1.0, 0.6, 10.0, 0.0)

% Allow pasing a vector with parameters
 if nargin==1
        d0 = k0(2);
        mu = k0(3);
        Mg = k0(4);
        sg = k0(5);
        l  = k0(6);
        q  = k0(7);
        MK = k0(8);
        sK = k0(9);
        rg = k0(10);
        h00 = k0(11);
        k0 = k0(1);
 end

% Implementation parameters
extinction_threshold = 1e-15;
branching_threshold = 1e-2;
branching_time_delay = 1000;
new_strain_fraction = 0.1; % Fraction of parental morph biomass allocated to mutant strain at
an evolutionary branching event.

plot_figures = 1;

time_stop = 1e50;

% First half are densities, second half are trait values
ic = [1 1 0 3];

options = odeset('Events', @events, 'RelTol', 1e-5, 'AbsTol', 1e-5);

last_branching_time = zeros(1, length(ic)/2);
time_start = 0;

if plot_figures
  figure(1)
```

```
  clf
end

done = 0;

while (not(done))

   [T, Y, TE, YE, IE] = ode15s(@evolve, [time_start time_stop], ic, options);
   n = length(ic)/2;

%     % Fitness landscape
   y = Y(end,:)
   x = y(1:n); % Densities
   r = y(n+1:2*n); % Trait values

   if plot_figures

      hold all
      plot (T, Y(:, n+1),'k--','LineWidth', 2)%,'Color'
      plot (T, Y(:, n+2:2*n),'k','LineWidth', 2)%,'Color'
      %xlim([300, 10^10]);
      set(gca, 'XScale', 'log','FontSize',16,'LineWidth', 2)
      box on

%%%
```

```
end

ESS_state = Y(end,:);

  function [tstart, ic] = update_system (T, Y, IE)

    y = Y(end,:);
    n = length (y)/2; %
    x = y(1:n); % Densities
    r = y(n+1:2*n); % Trait values
    r_bef = r;

    IE_all = IE;

      for i =1:length(IE)

        kk = 1;
        if IE(i) <= n
          % Extinction event
          x(IE(i)-(kk-1)) = [];
          r(IE(i)-(kk-1)) = [];
          kk=kk+1;
        else
            if IE(i)<=2*n && IE(i)>n
              YYY_here = y;
            % Evolutionary branching event
            % We now split the density of branching species in half
              focal_morph = IE(i) - n;

            % Update trait values
              f_prim = sel_grad(r, x);
              if f_prim(focal_morph) < 0
                r(end+1) = r(focal_morph) + branching_threshold;
              else
                r(end+1) = r(focal_morph) - branching_threshold;
              end

            % Update biomass
            prior_density = x(focal_morph);
            x(focal_morph) = prior_density*(1-new_strain_fraction);
            x(end+1) = prior_density*new_strain_fraction;

            % Update time of last branching
            last_branching_time(focal_morph) = T(end);
            last_branching_time(end+1) = T(end);
            end
          end
    end
```

```
    tstart = T(end);
    ic = [x, r];
end

function dy = evolve (t, y)
    n = length(y)/2;
    x = y(1:n); % Densities
    r = y(n+1:2*n); % Trait values

    % Demographic dynamics
    dx = x.*(per_capita_growth_rate(r',x'))';
    dy = [dx; 0.*dx];

    % Evolutionary dynamics
    epsilon = 0.3;
    dy(n+1:end) = (epsilon*sel_grad(r', x'))';
    dy(n+1) = 0.0; % resource does not evolve
end

function y = per_capita_growth_rate(r,x)

    Fij = 0.*r;
    Fji = 0.*r;

    for i=2:length(r)
        %%PredationGain
        N1 = Mg * l * exp(r-r(i)).*gamma1(r(i)-r).* x;
        Ni = N1';

        D1 = sum( Mg *(h(r-0.75*r(i)).*gamma1(r(i) - r).*x)' );
        Di = 1 + D1;
        Fij(i) = sum(Ni/Di);

        %%PredationLoss
        N1l = Mg * gamma1(r-r(i)).* x;
        N1l(1) = 0;
        Nil = N1l';


        [rk1,rk2] = meshgrid(r,r);
        [rj1,rj2] = meshgrid(r,r);

        ga11 = Mg * gamma1(rj2 - rk1);
        ga11(1,:) = 0;
        D1l = (ga11.*h(rk1 - 0.75*rj2))*x' ;
        Dil = 1 + D1l;

        Fji(i) = sum(Nil./Dil)   ;
    end
```

```
    predationGain = Fij;
    predationLoss = Fji;

    [rj,ri] = meshgrid(r,r);
    com = MK * K(ri-rj);
    com(1,:) = 0;
    com(:,1) = 0;
    competitionloss = com*x';

    mortality = d(r);

    y = -mortality + predationGain - predationLoss - competitionloss';

    % Correct the growth rate of the resource
    N1R = Mg * gamma1(r).* x;
    N1R(1) = 0;
    NiR = N1R';

    [rk1,rk2] = meshgrid(r,r);
    [rj1,rj2] = meshgrid(r,r);

    gaR = Mg * gamma1(rj2 - rk1);
    gaR(1,:) = 0;
    D1R = ((gaR.*h(rk1 - 0.75*rj2))*x')';
    DiR = 1 + D1R;

    FjiR = sum(NiR'./DiR)   ;
    y(1) = rg - FjiR - k0*x(1);
end

function y = fitness_landscape(m, r, x)
    % Returns fitness of mutant with trait value rm, assuming
    % residents have trait value r at densities x.
    R = repmat(r,length(m),1);
    X = repmat(x,length(m),1);
    z = ones(length(r),1);
    M = m' * z';
    [rk,rj] = meshgrid(r,r);

    %% Predation gain
    N1 = (Mg * l * exp(R - M) .* gamma1(M - R)) * x';
    D1 = (Mg *(h(R-0.75*M).*gamma1(M - R))) * x' ;
    Fij = N1./(1 + D1);

    %%Predation Loss
    X(:,1) = 0;
    N1l = Mg * gamma1(R - M).*X;
    D1l = (Mg *(h(rk-0.75*rj).*gamma1(rj - rk))) ;
    D1l(1,:) = 0;
    D1la = D1l*x';
```

```
    D1li = 1 + D1la;
    Fp = bsxfun(@rdivide, N1l',D1li);
    Fji = sum(Fp',2);

    Compe1 = (MK * K(M-R)) ;
    Compe1(:,1)=0;
    Compe = Compe1 * x';
    Morta = d(m');
    y = Fij - Fji - Compe - Morta;
end

function y = sel_grad(r, x)

    Fij = 0.*r;
    Fji = 0.*r;

    for i=2:length(r)
        %% PredationGain
        N1 = Mg * l * exp(r-r(i)).* gamma1(r(i)-r).* x;
        U = N1';

        N1_diff = Mg * l * exp(r-r(i)).* gamma_diff(r(i)-r).* x - Mg * l * exp(r-r(i)).*
gamma1(r(i)-r).* x;  %% modified bse of exp(r-r(i))
        U_diff = N1_diff';

        D1 = sum( Mg * (h(r-0.75*r(i)).*gamma1(r(i) - r).*x)' );
        V = 1 + D1;

        D1_diff = Mg * -0.75 *(h_diff(r-0.75*r(i)).*gamma1(r(i) - r).*x)' + Mg * (h(r-
0.75*r(i)).*gamma_diff(r(i) - r).*x)' ; %% Mg * S_diff(rk - rp)*(h(r-0.75*r(i)).*gamma1(r(i)
- r).*x)' +
        V_diff = sum(D1_diff);

        Fij(i) = sum((V.*U_diff - V_diff.*U)/(V.^2));

        %%PredationLoss
        N1l = Mg * gamma1(r-r(i)).* x;
        N1l(1) = 0;
        Ul = N1l';

        N1l_diff = - Mg * gamma_diff(r-r(i)).* x;
        N1l_diff(1) = 0;
        Ul_diff = N1l_diff';

        [rk1,rk2] = meshgrid(r,r);
        [rj1,rj2] = meshgrid(r,r);

        ga11 = Mg * gamma1(rj2 - rk1);
        ga11(1,:) = 0;
        D1l = 1 + ((ga11.*h(rk1 - 0.75*rj2))*x');
```

```
        Vl = D1l ;

        gaa = Mg * gamma_diff(rj2 - rk1);
        gaa(1,:) = 0;
        D1l_diff = (gaa.*h(rk1 - 0.75*rj2))*x' + (ga11.*h_diff(rk1 - 0.75*rj2))*x';
        Vl_diff = D1l_diff;
        Vl_diff = 0;

        Vl_dup = Vl;
        Fji(i) = sum((Vl.*Ul_diff - Vl_diff.*Ul)./(Vl_dup.^2));
    end

    [rj,ri] = meshgrid(r,r);
    com = MK * K_diff(ri-rj);
    com(1,:) = 0;
    com(:,1) = 0;
    competitionloss = com*x';

    y = -d_diff(r) + Fij - Fji - competitionloss';

end

function y = fitness_bis(rMut, r, x)
        %% PredationGain
        N1 = (Mg * l * exp(r-rMut).* gamma1(rMut-r).* x)';
        U = N1;

        N1_diff = (Mg * l * exp(r-rMut).* gamma_diff(rMut-r).* x)' - (Mg * l * exp(r-rMut).*
gamma1(rMut-r).* x)' ;
        U_diff = N1_diff;

        N1_bis = ((Mg * l * exp(r-rMut).* gamma_bis(rMut-r).* x)' - (Mg * l * exp(r-rMut).*
gamma_diff(rMut-r).* x)') - ((Mg * l * exp(r-rMut).* gamma_diff(rMut-r).* x)' - (Mg * l *
exp(r-rMut).* gamma1(rMut-r).* x)') ;
        U_bis =  N1_bis ;

        D1 = sum( Mg * (h(r-0.75*rMut).*gamma1(rMut - r).*x)' );
        V = 1 + D1;

        D1_diff = Mg * -0.75 * (h_diff(r-0.75*rMut).*gamma1(rMut - r).*x)' + Mg * (h(r-
0.75*rMut).*gamma_diff(rMut - r).*x)' ;
        V_diff = sum(D1_diff);

        D1_bis = Mg *0.75^2 * (h_bis(r-0.75*rMut).*gamma1(rMut - r).*x)' + Mg * (h(r-
0.75*rMut).*gamma_bis(rMut - r).*x)' - 1.5 * Mg * (h_diff(r-0.75*rMut).*gamma_diff(rMut
- r).*x)';
        V_bis = sum(D1_bis);

        V_dup = V;
```

```
        Fij = sum((V^2*((V * U_bis + V_diff * U_diff) - (V_bis * U + V_diff * U_diff)) -
2*V*V_diff*(V * U_diff - V_diff * U))/(V^4));%sum(Ni)/sum(Di);

        %%PredationLoss
        N1l = Mg * gamma1(r-rMut).* x;
        N1l(1) = 0;
        Ul = N1l';

        N1l_diff = - Mg * gamma_diff(r-rMut).* x;
        N1l_diff(1) = 0;
        Ul_diff = N1l_diff';

        N1l_bis = Mg * gamma_bis(r-rMut).* x;
        N1l_bis(1) = 0;
        Ul_bis = N1l_bis';

        [rk1,rk2] = meshgrid(r,r);
        [rj1,rj2] = meshgrid(r,r);

        ga11 = Mg * gamma1(rj2 - rk1);
        ga11(1,:) = 0;
        D1l = 1 + ((ga11.*h(rk1 - 0.75*rj2))*x');
        Vl = D1l;

        gaa = Mg * gamma_diff(rj2 - rk1);
        gaa(1,:) = 0;
        D1l_diff = (gaa.*h(rk1 - 0.75*rj2))*x' + (ga11.*h_diff(rk1 - 0.75*rj2))*x' ;
        Vl_diff = D1l_diff;
        Vl_diff = 0;

        gaaa = Mg * gamma_bis(rj2 - rk1);
        gaaa(1,:) = 0;
        D1l_bis = (gaaa.*h(rk1 - 0.75*rj2))*x' + 2 * (gaa.*h_diff(rk1 - 0.75*rj2))*x' +
(ga11.*h_bis(rk1 - 0.75*rj2))*x';
        Vl_bis = D1l_bis;
        Vl_bis = 0;

        Vl_dup = Vl;
        Fji = sum((Vl.^2.*((Vl .* Ul_bis + Vl_diff .* Ul_diff) - (Vl_bis .* Ul + Vl_diff .*
Ul_diff)) - 2*Vl.*Vl_diff.*(Vl .* Ul_diff - Vl_diff .* Ul))./(Vl_dup.^4));%sum(Ni)/sum(Di);

        com = MK * K_bis(rMut-r).*x;
        com(1) = 0;
        competitionloss = sum(com);

        mortality = d_bis(rMut);
        y = Fij - Fji - competitionloss - mortality;

    end
```

```
function y = h(x)
   y = h00*exp(x);
end

function y = h_diff(x)
   y = h00*exp(x);
end

function y = h_bis(x)
   y = h00*exp(x);
end

function y = d(r)
   y = d0 * exp(-q * r);
end

function y = d_diff(r)
   y = - q * d0 * exp(-q * r);
end

function y = d_bis(r)
   y = + q^2 * d0 * exp(-q * r);
end

function y = gamma1(x)
  y = 1/(sqrt(2*pi) * sg) * exp(-(x-mu).^2/(2*sg^2));
end

function y = gamma_diff(x)
  y = 1/(sqrt(2*pi) * sg) * (- 2 * (x - mu) ./ (2*sg^2)) .* exp(-(x-mu).^2/(2*sg^2));
end

function y = gamma_bis(x)
  T1 =  1/(sqrt(2*pi) * sg) * (- 2 * 1 ./ (2*sg^2)) .* exp(-(x-mu).^2/(2*sg^2));
  T2 =  1/(sqrt(2*pi) * sg) * (- 2 * (x - mu) ./ (2*sg^2)).^2 .* exp(-(x-mu).^2/(2*sg^2));
  y = T1 + T2;
end

function y = K(x)
   y = 1/(sqrt(2*pi) * sK) * exp(-x.^2/(2*sK^2));
end

function y = K_diff(x)
   y = 1/(sqrt(2*pi) * sK) * (-2*x/(2*sK^2)) .* exp(-x.^2/(2*sK^2));
end

function y = K_bis(x)
   T1 = 1/(sqrt(2*pi) * sK) * (-2/(2*sK^2)) .* exp(-x.^2/(2*sK^2));
   T2 = 1/(sqrt(2*pi) * sK) * (-2*x/(2*sK^2)).^2 .* exp(-x.^2/(2*sK^2));
   y = T1 + T2;
```

```
end

function [value, isterminal, direction] = events(t,y)
    % When value(i) is equal to zero, event i is triggered.
    % Convention: 1,...,n are extinction events while n+1, ..., 2n are
    % evolutionary branching events, event n+1 corresponds to the ESS
    % ccondition since the resource doesn't evolve.

    n = length(y)/2;
    x = y(1:n); % Densities
    r = y(n+1:2*n); % Trait values
    rbis=sort(r);
    min_dist = min(rbis(2:n)-rbis(1:n-1));

    value = 1.*y;

    % Check for extinction events
    for i=1:n
        if x(i) < extinction_threshold
            value(i) = 0;
        else
            value(i) = 1;
        end
    end

    % Check for evolutionary branching events
    f_prim = sel_grad(r',x');

    dx = x.*(per_capita_growth_rate(r',x'))';
    f_bis = 0.*r+1;
    for i=2:length(r)
        f_bis(i) = fitness_bis(r(i), r', x');
    end

    value(n+1) = 1; % resource does not evolve
    for i=2:n
        if (f_bis(i) > 0) && (2*abs(f_prim(i)/f_bis(i)) <min(branching_threshold,min_dist))
&& (t - last_branching_time(i) > branching_time_delay) %&& (max(abs(dx))<10^-6);%%
&& Varie<10^-10
            value(n+i) = 0;
        else
            value(n+i) = 1;
        end
    end
        comp=0;
        for i=2:n
            if (f_bis(i) < 0) && (abs(f_prim(i)) <0.000000000001)
                comp=comp+1;
            end
        end
```

```
        if (comp==n-1)
            disp ('we are here and ESS is reached')
            value(n+1)=0; %mark as an ESS
        end

    isterminal = 1+0.*y; % terminate after the first event
    direction = 0+0.*y;  % get all the zeros
  end

end
```